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INTEGRATED ISLAND ECOSYSTEM ECOLOGY IN HAWAII

SPATIAL DISTRIBUTION OF ISLAND BIOTA

INTRODUCTION

Part II, Chapter 6 of Proposed
Synthesis Volume for US/IBP Series

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PREFACE

This portion of the synthesis volume is being reproduced now because it is important that all synthesis volume contributors have these basic materials as they prepare their own contributions. Chapter 6, the subject matter of this report, follows the first five chapters that were contained in Technical Report 54 (Introductory Survey, Part I of the Synthesis Volume). It is expected that there will be some reworking of sections of this report as more data are analyzed and the integration needs of the entire synthesis part become more apparent. Chapter 6 is only the introduction to Part II. Additional material will include the altitudinal distribution of individual organism groups (Chap. 7) and their spatial integration along the Mauna Loa Transect (Chap. 8).

ABSTRACT

This report is a draft manuscript of the introduction to Part II of our proposed synthesis volume. As chapter 6, this introduction forms the continuation to Part I in Technical Report 54, which contains the first five chapters.

Part II, which is concerned with an analysis of the spatial distribution of island biota in an ecosystem context, is one of four major synthesis areas of the Island Ecosystems Integrated Research Program of the US/IBP. This report gives the conceptual and physical background to our distribution analysis along a transect on a high-island mountain, Mauna Loa. It further discusses current ecological theory of species distributions along environmental gradients and presents examples together with the analytical techniques that we adopted for all organism groups investigated in spatially integrated community samples.

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PART II. SPATIAL DISTRIBUTION OF ISLAND BIOTA

CHAPTER 6

INTRODUCTION

6.1 Reasons for Choice of Transect Approach

Distribution studies of biota and ecosystem components can be done at all geographic scales. Most distributional studies of island biota have been concerned with comparisons between islands and island groups, such as those of MacArthur and Wilson (1967). On large, oceanic islands, it is also useful to study biotic distribution patterns within the island itself. With this latter approach, emphasis is placed on understanding how the generally depauperate biota adapt, compete, and evolve. The former approach is generally given to a study of dispersal, establishment, and, to some extent, evolution.

In this investigation the within-island approach was chosen for a number of reasons. Primarily, it allows a study oriented toward examining the island ecosystems rather than separate organism-oriented studies. Such an investigation also could be carried out within the time limits given to the IBP studies, and the results would be expected to allow comparison with the other ecosystem-oriented IBP projects. The area selected for the spatial distribution analysis was Hawaii Volcanoes National Park (reasons are given in Part I, Section 5.2). Here, we concentrated our analysis along an existing mountain transect (transect 1 on Fig. 5.1).

A distribution study along a major mountain slope allows for comparisons with similar studies in continental mountain ecosystems. The approach ties into a general area of ecological theory that has its roots in the "ecological series" concept of Russian authors (e.g. Sukachev 1928), in the "ecological species group" derivation techniques of Ellenberg (1956, Mueller-Dombois and Ellenberg 1974), and in the environmental gradient approach of Whittaker (1967) that was developed in temperate, continental mountain systems.

Environmental gradient analysis is essentially a field-experimental approach. It utilizes the experimental principle of changing the environmental factor or factor complex to which one wishes to test a biological response, while attempting to hold all other factors constant. The latter is extremely difficult or next to impossible in field environments, and more often than not one finds that several factors change concomitantly, randomly, or even erratically. The goal is to select

sampling sites in such a way that the gradient inconsistencies are minimized. Whittaker (1956, 1960) achieved this by comparing only sites of similar physiographic position at different elevations.

In an altitudinal gradient analysis, the changing factor (or factor complex) is generally the climate. There are a number of other factors which may be kept constant so that the climatic influence may be observed. The particular selection of constant factors depends largely on the organisms being studied. For example, a well-drained substrate of similar geochemical composition or similar parent material may be important for vegetation studies while the availability of the same tree species may be important for studies of host-adapted insects.

By choosing an altitudinal gradient on an island, it is also possible to make comparisons of the spatial distribution of native vs. exotic species and their deviations from continental gradients. Such an approach also provides an opportunity to critically examine other trends. The temporal changes in the abundance of organisms along a climatic gradient is one example (covered in Part III). The study of the genetic structure of the organisms along the gradient should also help reveal the pattern of their micro-evolution (covered in Part V). For these sorts of reasons, the altitudinal gradient analysis approach was seen as being ideally suited to provide answers to several of the initial working hypotheses (stated in Part I).

In Hawaii quantitative studies of species distributions have more than an academic interest. Because of the high proportion of rare and endangered species native to the islands, particular attention is given to their preservation. This is expressed in the establishment of natural areas and by various efforts to expand the present range of native species. The implications of our distribution studies to the scientific management of these programs will be discussed in Part VII.

6.2 The Mauna Loa Transect as a Case Example of a Major Environmental Gradient

Extensive mountain slopes, suitable for environmental gradient analysis, may be found in nearly all climatic regions of the world. They occur in continental as well as insular settings. They usually display a reasonably self-evident altitudinal zonation of vegetation belts. For example, the altitudinal vegetation zones in Hawaii, on Mauna Loa and Mauna Kea, are closely comparable to those of other tropical mountains of the world (Troll 1959, Walter 1971).

Mauna Loa is geologically a very young mountain. Its biota and community formation can thus be compared with the biota and community formation of older mountains with similar elevations and climatic zonations. As a young volcanic

mountain, Mauna Loa is typically shield-shaped, meaning that it has a very gradual smooth slope descending radially in all directions from the summit. There are no dissected valleys, streams, or tributaries, and topographic variations within the same altitudinal segment are so minor that they have no significant effect on the vegetation. Thus, the problem of eliminating the effect of a "topographic moisture gradient" (sensu Whittaker 1956, 1960) in altitudinal gradient analysis does not exist for such a mountain. All sites within a given elevational segment are well-drained and of uniform topographic position. This makes for little complication in site selection. The only major "discontinuities" are caused by a few intercepting lava flows of recent historical origin (i.e. issued within the last 200 years). These flows are narrow enough so that they were avoided in sampling. The sampling sites are located on the older, prevailing surfaces and are comparable in the sense that they are from volcanic materials of similar geochemical composition (Macdonald and Abbott 1970). Any substrate differences that may occur can be interpreted in terms of physical factors (see Section 6.5).

Important differences in the vegetation formations along the transect slope can be attributed to climate. Evidence for this is given by the close similarity of vegetation formations along a parallel east flank transect on Mauna Kea (Mueller-Dombois and Krajina 1968), a mountain of much greater age. Both temperature and rainfall decrease upslope in a similar pattern on both mountains. Rainfall on these mountains is controlled mostly by the tradewinds so that a given slope direction is exposed to a spatially rather stable atmospheric moisture pattern. The east flank of Mauna Loa, which was chosen for our transect analysis, is exposed to the NE tradewinds. It thus is representative of the wet side of a major tradewind-intercepting mountain.

6.3 The Mauna Loa Transect in Relation to the Other Park Transects

The geographic location of the Mauna Loa Transect is shown as transect 1 on Figure 5.1. It extends from 12,000 feet (3660 m) near the summit of Mauna Loa, downslope on its east flank in the Park to 3920 feet (1190 m) near the summit of the Kilauea Crater. Transect 1 spans a distance of 22 miles (35 km). The transect cuts through four of the six environmental sections recognized for the Park (Mueller-Dombois and Fosberg 1974). The four sections are: (1) the alpine section, from the top of Mauna Loa to 8500 feet (2590 m), (2) the subalpine section, downslope to 6700 feet (2040 m), (3) the montane seasonal section, downslope to 3800 feet (1160 m) and south of transect 1, and (4) the montane rain forest section,

in part covered by the east end of transect 1 (see Fig. 6.1). The other two environmental sections in the Park, not traversed by the Mauna Loa Transect are: (5) the submontane seasonal section and (6) the coastal lowland section; both are on the south slope of Kilauea Volcano. These sections are traversed by transects 2 to 5 on Figure 5.1. These transects were not included in the integrated analysis. A description of all six Park transects is given by Mueller-Dombois (1966:396-437).

6.4 Profile Diagram and Photographs of Ecosystems

The profile diagram on Figure 6.2 indicates the general relationships of climate, vegetation, and substrate along the Mauna Loa Transect. Twelve segments are shown. These were defined on the basis of mappable differences in vegetation structure and dominant species along the slope (Mueller-Dombois 1966, 1967). The combination of the vegetation types with their environmental components (climate, topographic position, and soil-substrate) allows them to be recognized as ecosystem types.

They are named as follows:

Segment 1 Alpine stone desert
Segment 2 Rhacomitrium moss desert
Segment 3 Sparse alpine scrub
Segment 4 Alpine aggregate-scrub
Segment 5 Metrosideros tree line ecosystem
Segment 6 Open subalpine Metrosideros scrub-forest
Segment 7 Mountain parkland (formed by Acacia koa tree communities, Styphelia shrub communities and grass communities)
Segment 8 Acacia koa-Sapindus savanna
Segment 9 Closed kipuka forest (segment 8 interdigitates locally with segment 9)
Segment 10 Open Metrosideros dry forest
Segment 11 Open Metrosideros rain forest
Segment 12 Closed Metrosideros rain forest

The following four plates (Fig. 6.3 to 6.6) and their legends provide a brief description of the twelve segments or ecosystem types.

6.5 Altitudinal Distribution of Major Site Factors

From a transect-wide viewpoint the major site factors can be grouped into three environmental components: climate, soil-substrate, and mechanical influences.

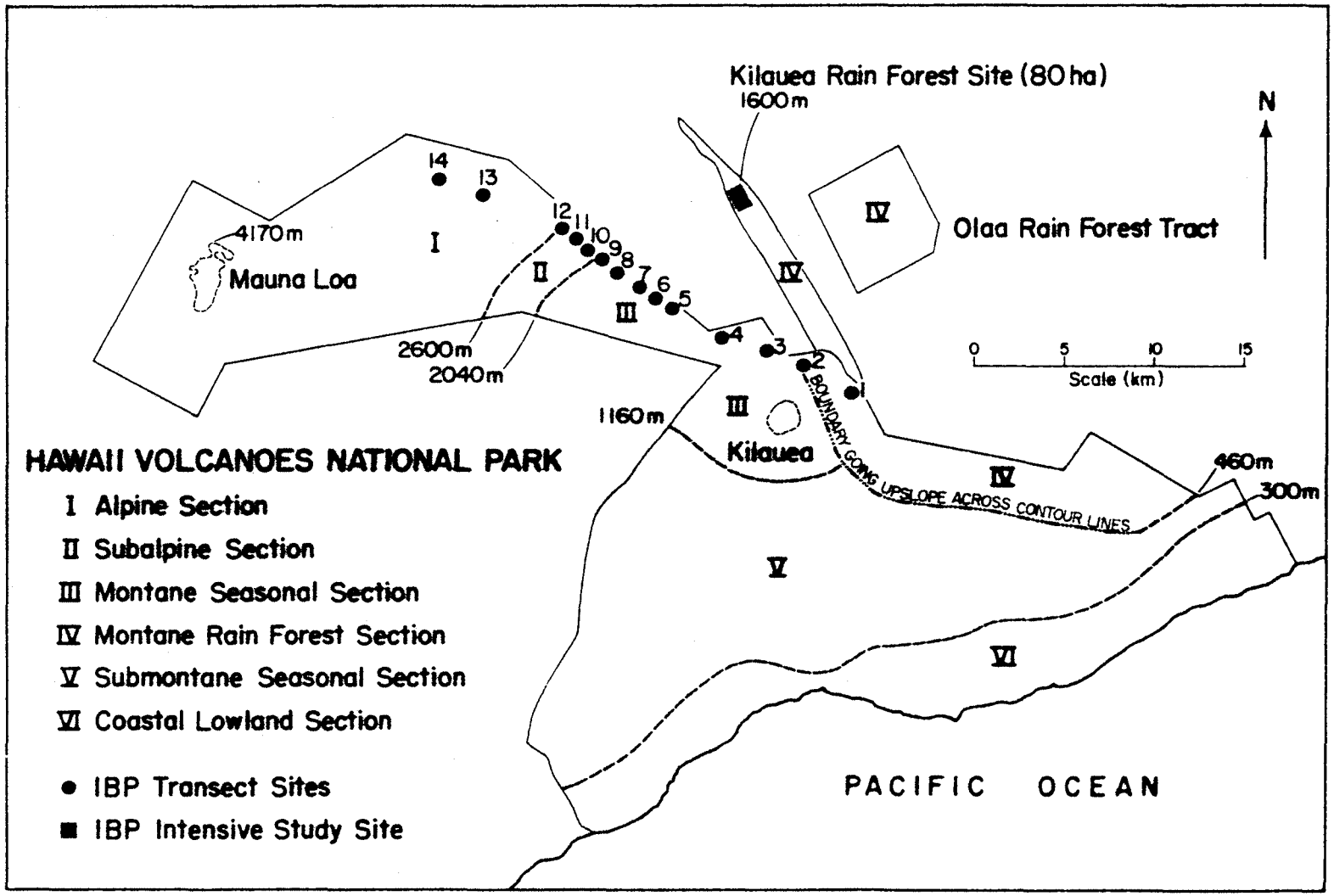


FIG. 6.1. Map of Hawaii Volcanoes National Park showing the six environmental sections, the 14 Mauna Loa Transect sampling sites, and the Kilauea Rain Forest site. (For broader overview see Fig. 5.1).

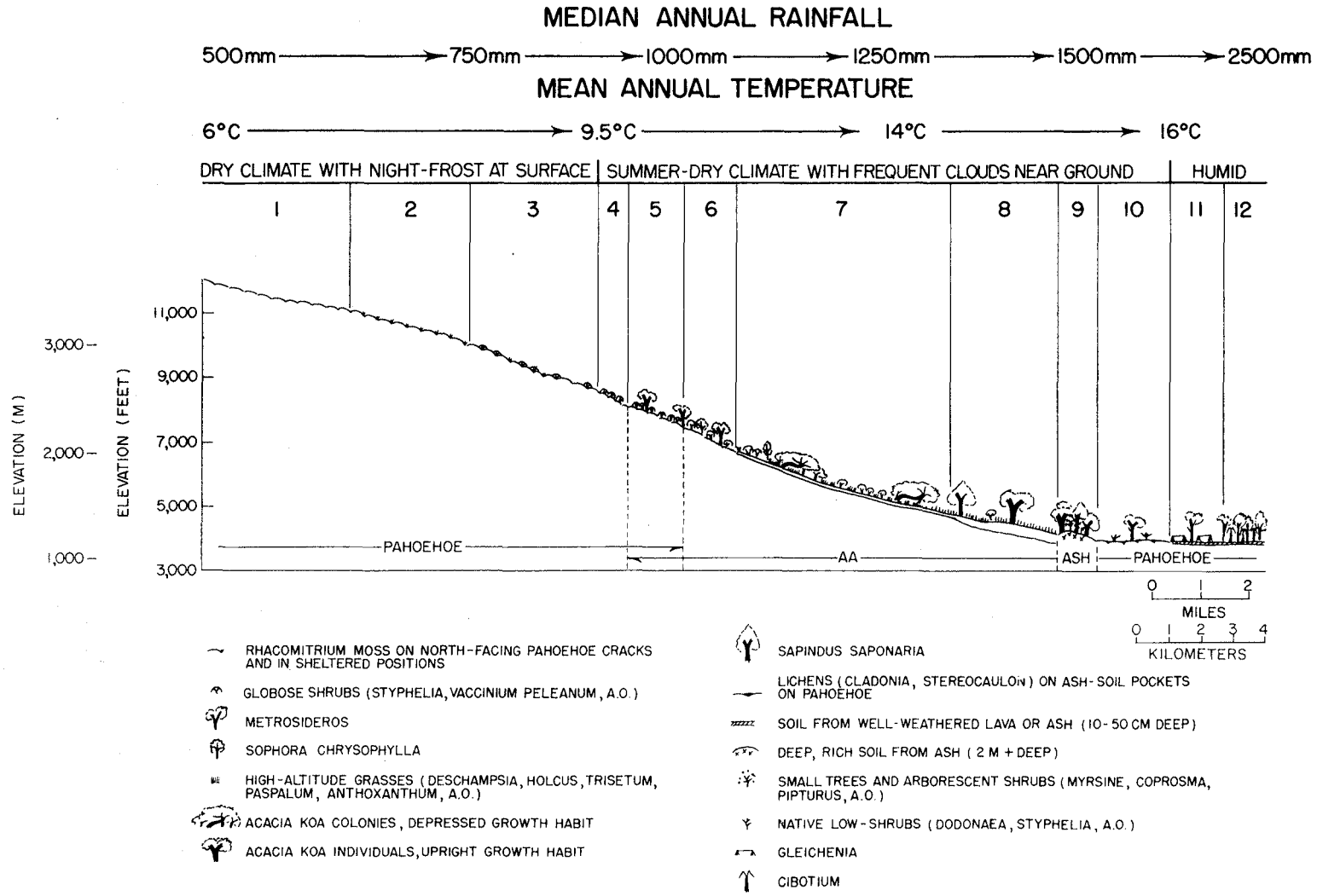


FIG. 6.2. Profile diagram of the Mauna Loa Transect. For geographic location see Fig. 5.1, transect 1.

Fig. 6.3-1. View of Mauna Loa summit (13,680 ft = 4170 m) and its upper east flank forming the skyline to the left downslope to about 10,000 feet (3050 m). Photograph taken from summit area of Mauna Kea, 35 km away. The light and dark colored areas are lava flows of different kinds and ages. The light colored fields are pahoehoe flows (mostly smooth pavement type or ropy rock plates with cracks); the dark colored fields are mostly a'a flows (rock rubble type lava). The older flows are oxidized and light brown in color. They show up grayish on the photograph.

Fig. 6.3-2, Segment 1. Vegetationless stone desert extending from summit to about 11,000 feet (3350 m). Here substrate is composed of ropy pahoehoe lava.

Fig. 6.3-3, Segment 2. Rhacomitrium moss desert, from 11,000 to 10,000 feet (3050 m). The moss R. lanuginosum var. pruinosum is found on the older, oxidized lava. Here it occurs only in very scattered small colonies in the tradewind-facing (northward oriented) crevices. The white hyaline tips give the moss a snow-like appearance.

Fig. 6.3-4, Segment 3. Vaccinium-Styphelia low-scrub desert, or sparse alpine scrub, from 10,000 to 8550 feet (2600 m). The two native shrubs Vaccinium peleanum and Styphelia douglasii grow here in widely scattered formation. Additional species are the ferns, Pellaea ternifolia and Asplenium trichomanes and two native grasses Agrostis sandwicensis and Trisetum glomeratum, which are extremely sparse. The dominant surface feature is still the oxidized pahoehoe lava.

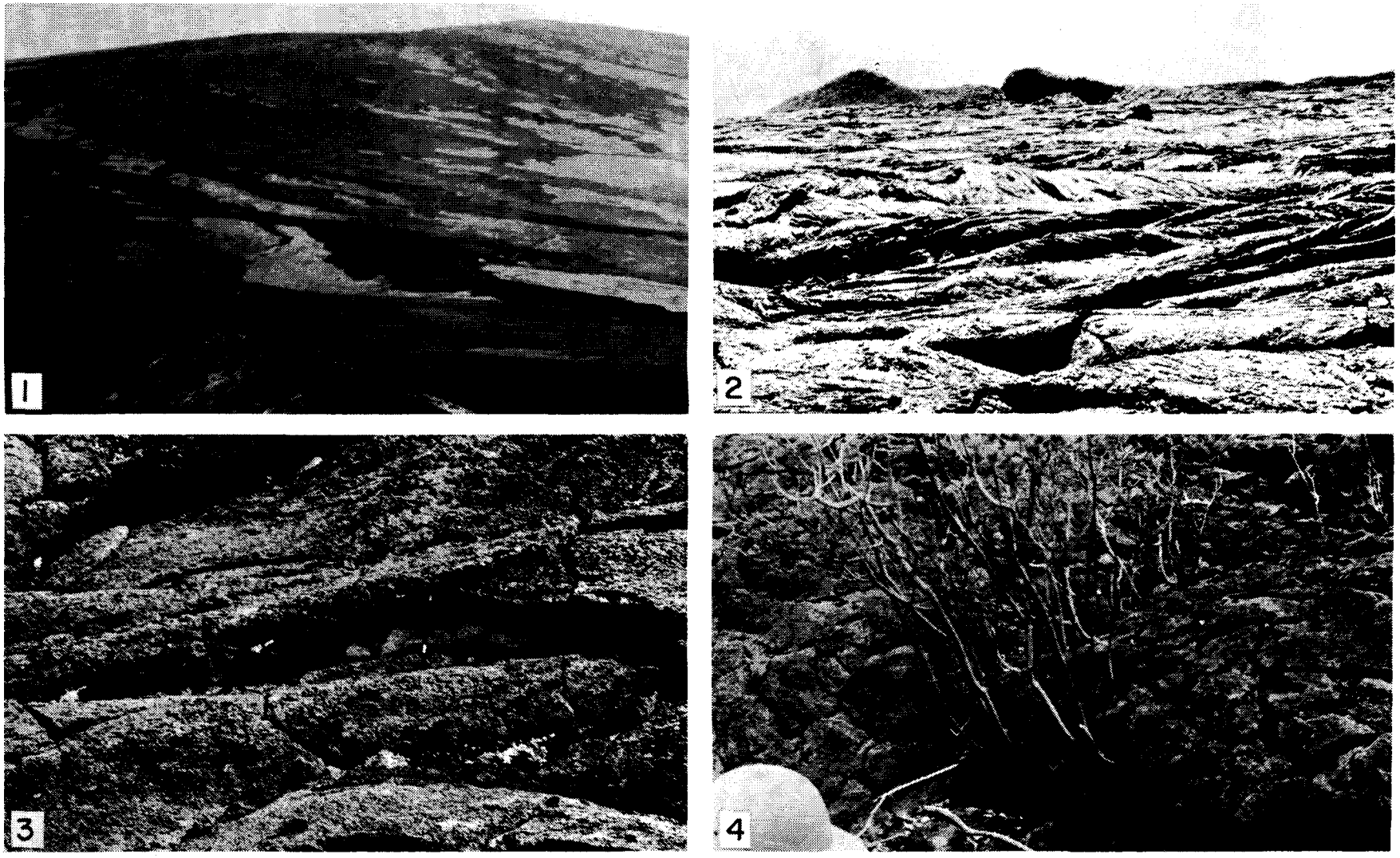


FIG. 6.3. Alpine Section (Mauna Loa Transect). Dry, cool climate: 500-750 mm rainfall per year; 6-9.5°C mean air temperature; nocturnal ground frost each night of the year. Profile segments 1-3 on Figure 6.2.

Fig. 6.4-1, Segment 4. Scattered globose aggregate-scrub, from 8550 to 8200 feet (2500 m). Additional native shrub species occur: Dodonaea viscosa and Coprosma ernodeoides, which often grow aggregated in clumps with Vaccinium and Styphelia. The native grass Trisetum glomeratum grows sparsely on the fine soil-dust collected around the shrub clumps (on the photograph).

Fig. 6.4-2, Segment 5. Metrosideros tree line ecosystem, from 8200 feet (2500 m) to 7500 feet (2290 m). Widely scattered Metrosideros collina subsp. polymorpha var. incana trees grow 4-5 m tall, with native shrub species aggregated beneath.

Fig. 6.4-3, Segment 5. The Hawaiian silversword (Argyroxiphium sandwicense) thrives in the tree line ecosystem, but here it was planted by the National Park Service. The native bunchgrass, Deschampsia australis is in the foreground. The shrubs are mostly Styphelia douglasii (on the photograph).

Fig. 6.4-4, Segment 6. Open Metrosideros scrub-forest, from approximately 7500 feet (2290 m) to 6700 feet (2040 m). The change from segment 5 to 6 is very gradual. Metrosideros trees grow less widely scattered than in the tree line ecosystem and the shrubs become denser downslope. At approximately 7500 feet (2290 m) elevation, the lava substrate is no longer the dominant surface feature. Instead, shrubs cover most of the surface. The native legume tree Sophora chrysophylla occurs scattered in the lower part of this segment (not on the photograph).

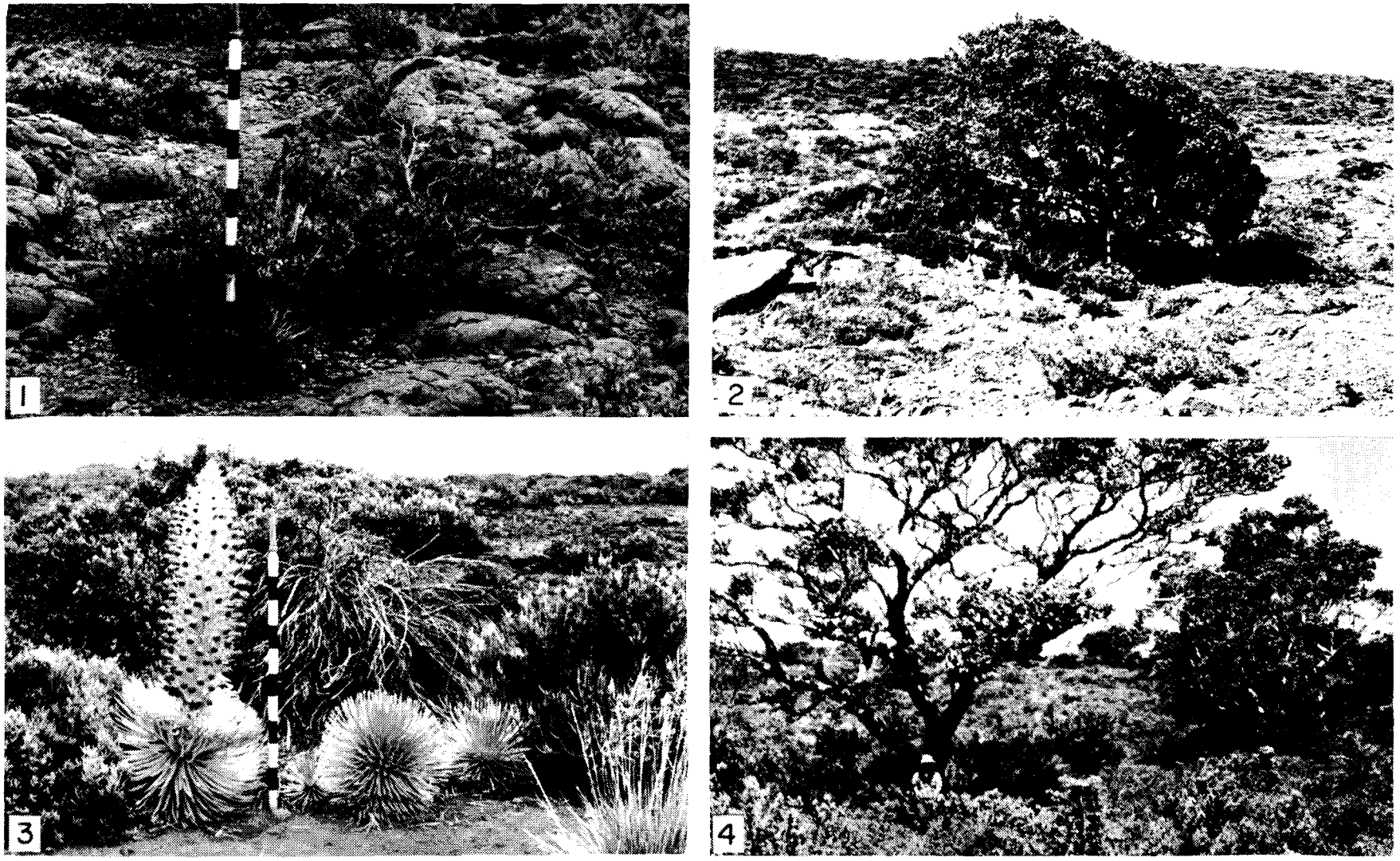


FIG. 6.4. Subalpine Section (Mauna Loa Transect). Summer-dry climate: ~1000 mm rainfall per year; 9.5-12°C mean air temperature; frequent clouds near ground. Profile segments 4-6 on Figure 6.2.

Fig. 6.5-1, Segment 7. Mountain parkland ecosystem, from 6700 feet (2040 m, at end of Mauna Loa Strip Road) to approximately 4500 feet (1370 m). This ecosystem contains three distinct communities: Acacia koa tree colonies, tall-shrub communities of mixed Styphelia douglasii and Dodonaea viscosa bushes, and grassland. The latter forms the matrix surrounding the two types of woody plant communities. The grassland is dominated locally by the native Deschampsia australis, but where disturbed by pigs, it is dominated by the European weedgrass Holcus lanatus.

Fig. 6.5-2, Segment 8. Acacia koa-Sapindus savanna, from 4500 feet (1370 m) to 4000 feet (1220 m). The major difference from the mountain parkland ecosystem is the absence of the Styphelia-Dodonaea tall-shrub communities. Also several other introduced grass species become dominant, particularly Paspalum dilatatum. The dominant tree is Acacia koa which is occasionally associated with Sapindus saponaria (not on photograph).

Fig. 6.5-3, Segment 9. Closed kipuka forest. The Hawaiian word kipuka stands for island of vegetation surrounded by more recent lava flows. The taller trees (up to 25 m) are the same as in the savanna. A well-developed lower tree layer is comprised of several species including Myrsine lessertiana, Coprosma rhynchocarpa, Psychotria hawaiiensis, Osmanthus sandwicensis, Sophora chrysophylla, Pipturus albidus, and others. Microlepia setosa is a locally dominant fern in the undergrowth (on photograph). A detailed description is given by Mueller-Dombois and Lamoureux (1967). This closed mesic forest interdigitates locally with segment 8, between 4250 and 4000 feet (1300-1220 m).

Fig. 6.5-4, Segment 10. Open Metrosideros-lichen forest with native low-shrubs, at approximately 3950 feet (1200 m) elevation. Metrosideros collina subsp. polymorpha var. incana grows in the old pahoehoe cracks that appear to control the density of stocking. The trees are rather short (3-10 m). The depressions between outcropping pahoehoe blocks are covered with pockets of finer soil and ash which support a poor growth of lichens (Cladonia spp. and Stereocaulon), grasses and herbs (Andropogon virginicus, Bulbostylis capillaris, Pteridium aquilinum). Most of the surface is covered by native shrubs, Dodonaea viscosa, Styphelia tameiameiae, Raillardia scabra, Vaccinium reticulatum, and Coprosma ernodeoides.

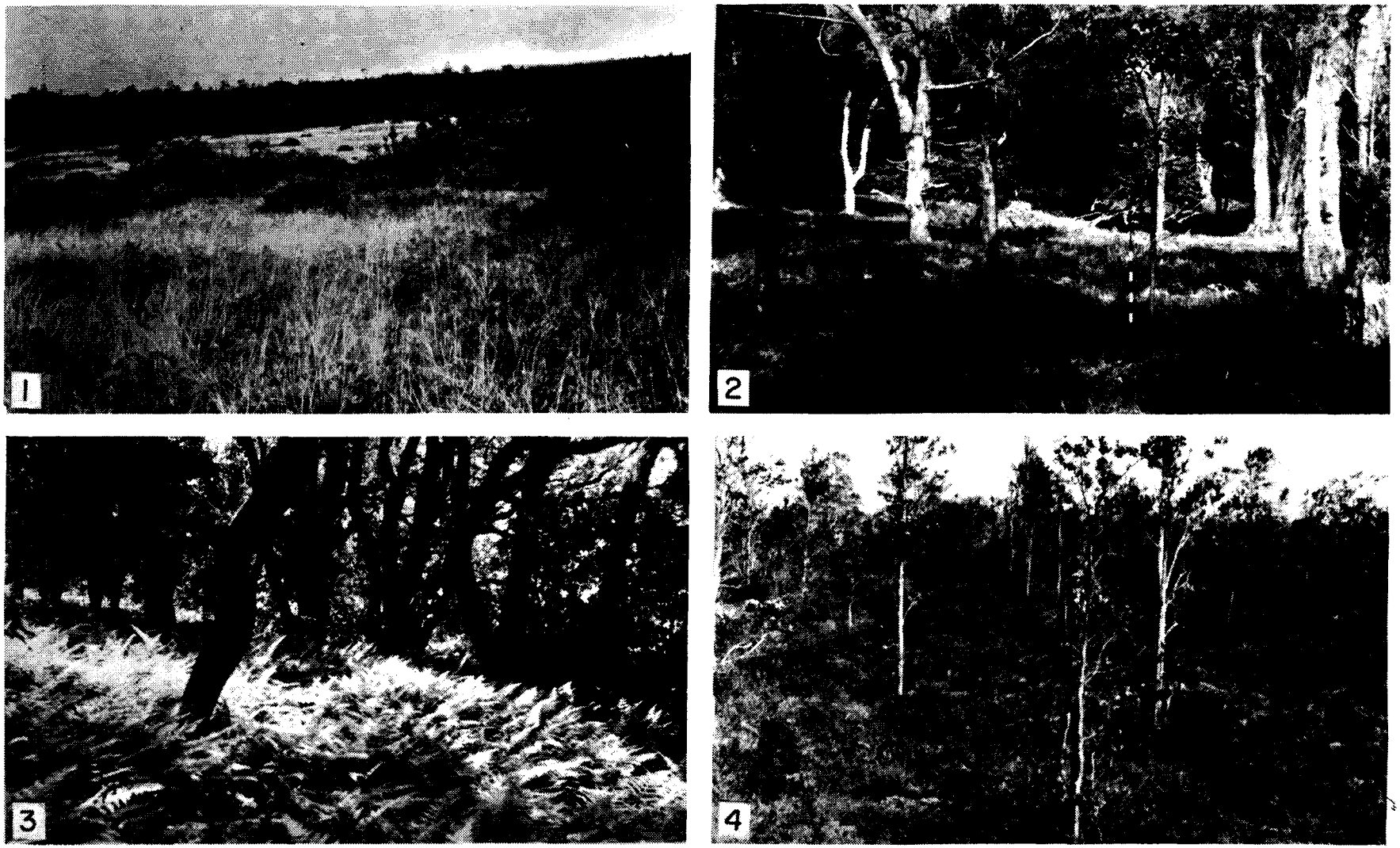


FIG. 6.5. The Montane Seasonal Section (Mauna Loa Transect). Summer-dry climate: 1100-1500 mm rainfall per year; 12-16°C mean air temperature; frequent clouds near ground. Profile segments 7-10 on Figure 6.2.

Fig. 6.6-1, Segment 11. Open Metrosideros-Gleichenia forest, at approximately 3950 feet (1200 m) elevation. Tree growth is similar to preceeding type, but undergrowth is dominated by the matted fern, Gleichenia (= Dicranopteris) emarginata. In places not dominated by the fern, one can find individuals of the herbs Dianella sandwicensis, Hedyotis centranthoides, Lycopodium cernuum, and Andropogon virginicus. The woody fern, Sadleria cyatheoides, is frequent also.

Fig. 6.6-2, Segment 12. Closed Metrosideros-Cibotium forest, at 3920 feet (1190 m). This is the prevailing montane rain forest type in the Park. It is characterized by a stand of relatively even-sized Metrosideros trees with diameters at breast height of 40-65 cm and uniform crown-canopy heights from 14 to 20 m. Tree boles are rather naked and rarely covered with epiphytes. A distinct lower stratum is formed by the tree ferns (Cibotium spp.). Associated smaller trees include Myrsine lessertiana, Ilex anomala, Coprosma ochracea, and Cheirodendron trigynum. Common shrubs are Vaccinium calycinum, Cyrtandra platyphylla, Broussaisia arguta, Pipturus albidus. Herbs frequently found include Gahnia gahniaeformis, Briza minor, Isachne distichophylla, Hedyotis centranthoides, Lycopodium cernuum, and Peperomia spp.

Fig. 6.6-3, Segment 12. Inside view of the rain forest near Thurston Lava Tube. Tree fern (Cibotium glaucum) behind the meter stake, Sadleria cyatheoides in foreground, left.

Fig. 6.6-4, Segment 12. View to Kilauea Iki Crater floor in rain forest section near end of transect 1.

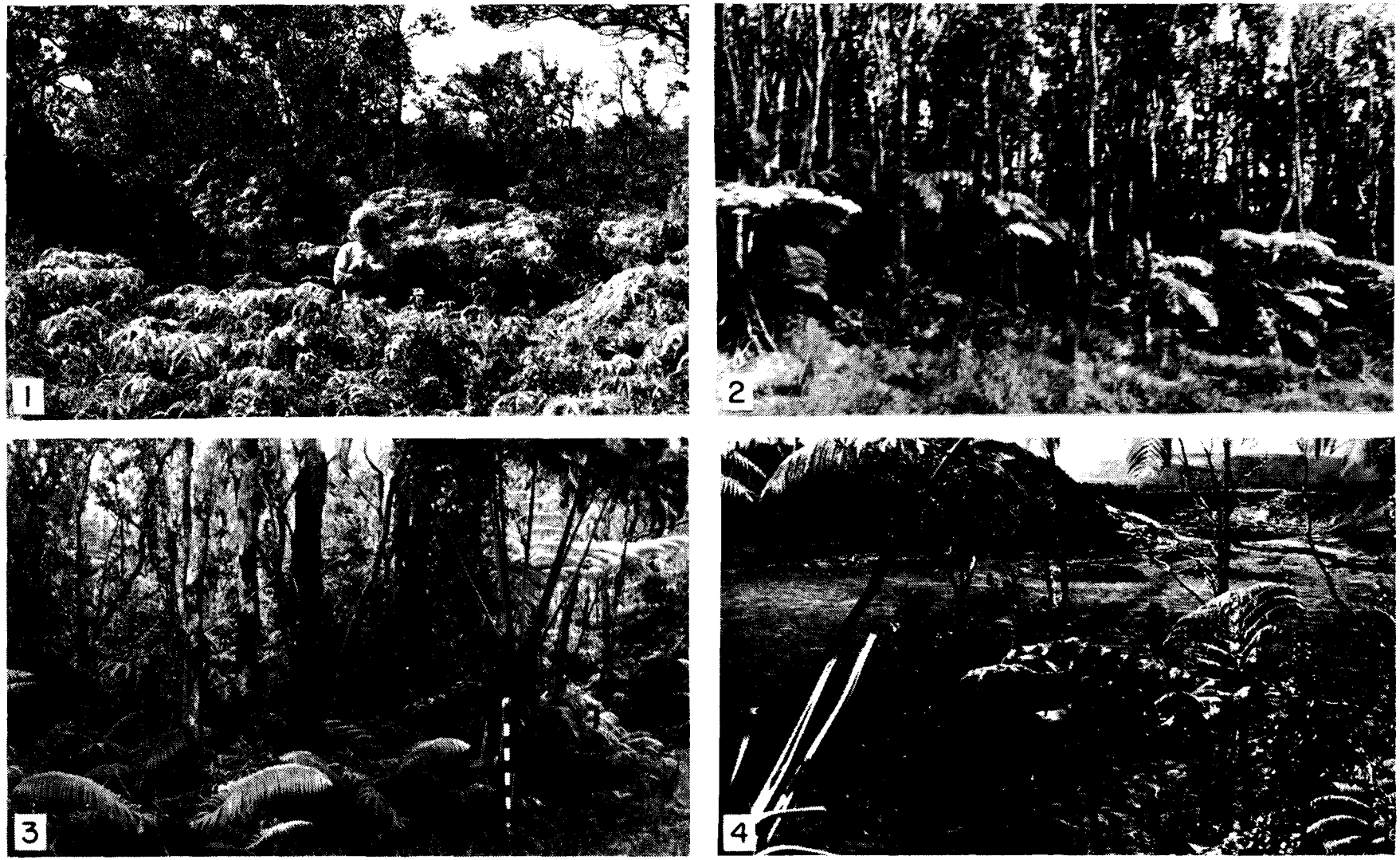


FIG. 6.6. Montane Rain Forest Section (Mauna Loa Transect). Year-round humid climate: 2000-2500 mm rainfall per year; ~16°C mean air temperature. Profile segments 11 and 12 on Figure 6.2.

6.5-1 Climate. Two important climatic factors form continuous gradients along the transect: median annual rainfall and mean annual temperature. The relationship of both these factors are indicated at various points along the transect on Figure 6.2. The general trend is for the median annual rainfall to increase from 500 mm in the alpine section downslope along the transect to 2500 mm in the montane rain forest section. The mean annual air temperature (as recorded in meteorological shelters 1.5 m above the ground) increased downslope from 6°C in the alpine section to 16°C in the montane sections of the transect.

The mean monthly variation of these two parameters can be gleaned from the climate diagrams on Figure 5.1. In the montane rain forest section, the average monthly rainfall is above 100 mm except in June, when the rainfall may drop to 80 mm (Fig. 5.1, Hawaii National Park Headquarters Station). In the mountain parkland (segment 7 on Fig. 6.2), there is a pronounced dry season in June when the rainfall curve touches or even drops below the mean monthly temperature curve (Fig. 5.1, Kekekaniho). Near the top end of the transect in the alpine section, a second dry season occurs during September (Mauna Loa Observatory).

The variability of the rainfall from year to year can be seen both in changes in the annual amounts and in changes in the monthly distribution patterns. This latter aspect is discussed in Part III. Considerable variation in the annual rainfall totals was seen during the three years of intensive sampling (1972-1974); the mean standard deviation of the annual rainfall sums for three IBP sites (4, 6, and 9) was 214 mm (Bridges and Carey TR 22, TR 38, TR 59).

The mean monthly temperature curve forms almost a straight line at each station indicating tropical insular climates at all elevations (Fig. 5.1). The warmest months are August and September and the coolest January and February, but the mean monthly temperature range between summer and winter is generally within 4°C. The daily temperature range is much greater, and varies from about 18°C at high elevations to 5°C near sea level. At Hawaii National Park Headquarters (near the low end of the transect) the mean daily temperature range is about 15°C. In the alpine section, freezing air temperatures occur from November through March as indicated by the fine dotted line below the mean monthly temperature curve on the Mauna Loa Observatory diagram (Fig. 5.1). Nocturnal ground frost temperatures were recorded during the warmest month of the year (August 1966, Mueller-Dombois and Krajina 1968) on the east flank of Mauna Loa down to 8600 feet (2600 m).

Several other climate parameters are also of interest as they vary along the transect. Fog drip under trees is a common phenomenon along the transect from the

tree line ecosystem at 8200 feet (2500 m) downslope through the mountain parkland; this includes the entire climatic zone defined on Figure 6.2 as summer-dry climate with frequent clouds near ground. Fog drip was measured by Juvik and Perreira (TR 32) along the transect with louvered screen cylinders of 2691 cm^2 surface area mounted 3 m above ground level. They found that fog drip added 65% to the rainfall at the tree line at 8200 feet (2500 m) on Mauna Loa. The contribution of fog drip decreased above and below this point. In the savanna (Fig. 6.2, segment 8) it was 49%. In terms of absolute fog interception the maximum water yield was recorded in the mountain parkland at 5200 feet (1580 m) elevation, where 638 mm of fog drip water was collected over a period of 7 months (October through April 1972). Thus, one may conclude that the trees and the plants growing under them in the tree line ecosystem receive at least 1.65 times the annual rainfall amount shown on Figure 6.2; in the mountain parkland they may receive about 1.5 times the amount. The exact amounts vary, of course, with the height and surface area of the tree, its branching and foliage arrangement, and other factors affecting condensation.

Pan evaporation rates for three transect sites have recently been determined by Clark, Austring, and Juvik (1975). Their data show a generally increasing rate of evaporation from 2.60 mm per day in segment 5 (the open Metrosideros scrub forest in the subalpine section) to 3.18 mm per day in segment 10 (the open Metrosideros-native scrub lichen forest in the lower end of the montane seasonal section). These data are based on 98 days of recording between July 1974 and May 1975.

6.5-2 Soil-Substrate. The major substrate types are indicated on Figure 6.2 as pahoehoe, a'a, and ash.

Pahoehoe is the prevailing substrate in the alpine section along the transect from segments 1 through 5. Pahoehoe is the type of lava that is particularly hot (1000°C) and liquid during the time of extrusion, when it flows like a slow-moving river before it cools down in situ. The cooling results in an uneven pavementlike surface. Several variations of pahoehoe have been described by Jones (1943). The main plant substrate is made up of the many cracks, folds, and fissures occurring between the bedrock slabs of the pahoehoe (Fig. 6.3, photographs 3 and 4). Only the oxidized, reddish brown or buff colored lava, which is the oldest and prevailing substrate, was included in the transect sampling. A few recent lava flows that occur here and there along the transect (such as shown in photograph 2 on Fig. 6.3) were excluded from the analysis. The cracks and fissures in the pahoehoe are so

numerous in this upper area of the transect that the scattered occurrence of shrubs (in segment 3, Fig. 6.2) cannot be explained as a lack of suitable substrates for plant growth. Instead the sparse growth appears to be a function of climate (low rainfall and low temperature) and geological recency of the substrate. Over long periods of time an increase in the density of the vegetation can be expected. This conclusion is based on comparisons of the vegetation cover at similar altitudes and in similar climates in other tropical mountains (Mueller-Dombois and Krajina 1968, Walter 1971).

In segment 5 (tree line ecosystem) the profile diagram (Fig. 6.2) shows an overlap of the two major types of lava--pahoehoe and a'a. A'a lava consists of individual rock chunks of various sizes, ranging mostly between 5 and 30 cm in diameter. These rock chunks are loosely stacked up in the form of a sheet, usually less than 1 m deep, above a solid pahoehoe-type core (Macdonald 1945). The fissures between the rock chunks are filled with fines (mostly from volcanic ash) along the Mauna Loa Transect. On first observation, it seemed that the upper limit of tree growth was correlated with the a'a lava. However, subsequent observations revealed that the first trees forming the tree line on Mauna Loa occur also on pahoehoe. Such a situation is shown on photograph 2 of Figure 6.4. A'a lava prevails throughout the middle section of the transect from the subalpine open scrub forest through the savanna (segments 6 through 8, Fig. 6.2).

In the same direction downslope there is a gradual increase of fines from volcanic ash. In the tree line ecosystem most lava cracks are already filled, and there are a few scattered pockets of fine, yellow dustlike ash on the pahoehoe surface (such as shown in the foreground on photograph 3, Fig. 6.4). Such ash pockets occur throughout segment 6, but the general surface is strewn with a'a rocks and the spaces between the rock chunks are filled almost everywhere with fine soil from ash. The volume of ash increases further downslope, where it forms initially a thinly overlying soil blanket (10-25 cm deep) in the upper part of the mountain parkland. This soil blanket is frequently interrupted by lava rock outcrops. Further downslope, rock outcrops become less frequent until they disappear entirely in the savanna. The ash blanket in the savanna is generally over 70 cm deep. The kipuka forests in segment 8 have very deep soils (in places over 5 m deep) that developed from ash dunes (Mueller-Dombois and Lamoureux 1967). The same applies locally to the savanna, which interdigitates with the closed kipuka forest in segment 9. More detailed soil variations from the alpine section to the kipukas are described by Mueller-Dombois (1966), but the general trend is

one of an increasing number of soil pockets from the alpine through the subalpine section downslope to an area of a shallow discontinuous ash blanket (in the upper mountain parkland) becoming a more continuous ash blanket (in the lower part) that increases in depth to over 70 cm in the savanna.

East of the deep soil savanna and kipuka, the substrate changes abruptly at the border to the open Metrosideros dry forest (segment 10, Fig. 6.2). Here again, the prevailing substrate is pahoehoe with a shallow, highly discontinuous ash blanket. The substrate is physically not unlike that of the subalpine open scrub-forest (segment 6) were it not for the difference in the outcropping lava type. Further eastward, the ash blanket again becomes continuous in the open rain forest (segment 11), and it reaches depths greater than 50 cm in the closed rain forest (segment 12).

The original chemical composition of the lava types and ash were all very similar, since they originated from the same source of magma. However, the pahoehoe and a'a along the slope originated from the Mauna Loa Volcano, while the ash blanket through the mountain parkland and savanna and the pahoehoe at the east end of the transect originated from the Kilauea Volcano.

The parent rock material is basaltic, showing relatively high amounts of calcium (about 10%) and magnesium (6-10%). The original silicon content is very high (near 50-70%). It drops in the course of weathering and becomes very low in older rain forest soils. But all soils along the Mauna Loa Transect are geomorphologically very recent and there is as yet little secondary clay formation. According to the soil order classification given in Chapter 3, the transect soils represent four of the 11 soil orders found in the Hawaiian Islands. The four are Lithosols (throughout the alpine and subalpine section), Entisols (the mountain parkland soil), Mollisols (the savanna and Kipuka soils), and Histosols (in the montane rain forest section).

The organic content in the surface soil contains about 12-15% carbon in the rain forest soils and the pH is between 4 and 5. Throughout the savanna and mountain parkland the organic content is similarly high, ranging from 10 to 15%; but the pH is less acid, ranging generally from 5.5 to 6.5 (Mueller-Dombois 1966).

Soil analyses on the mineral abundances are shown for the transect profile in Figure 6.7. The relative abundances have been plotted in such a way as to allow their comparison with the normal ranges of mineral abundances established for optimal plant growth (M. Stoner, unpublished data).

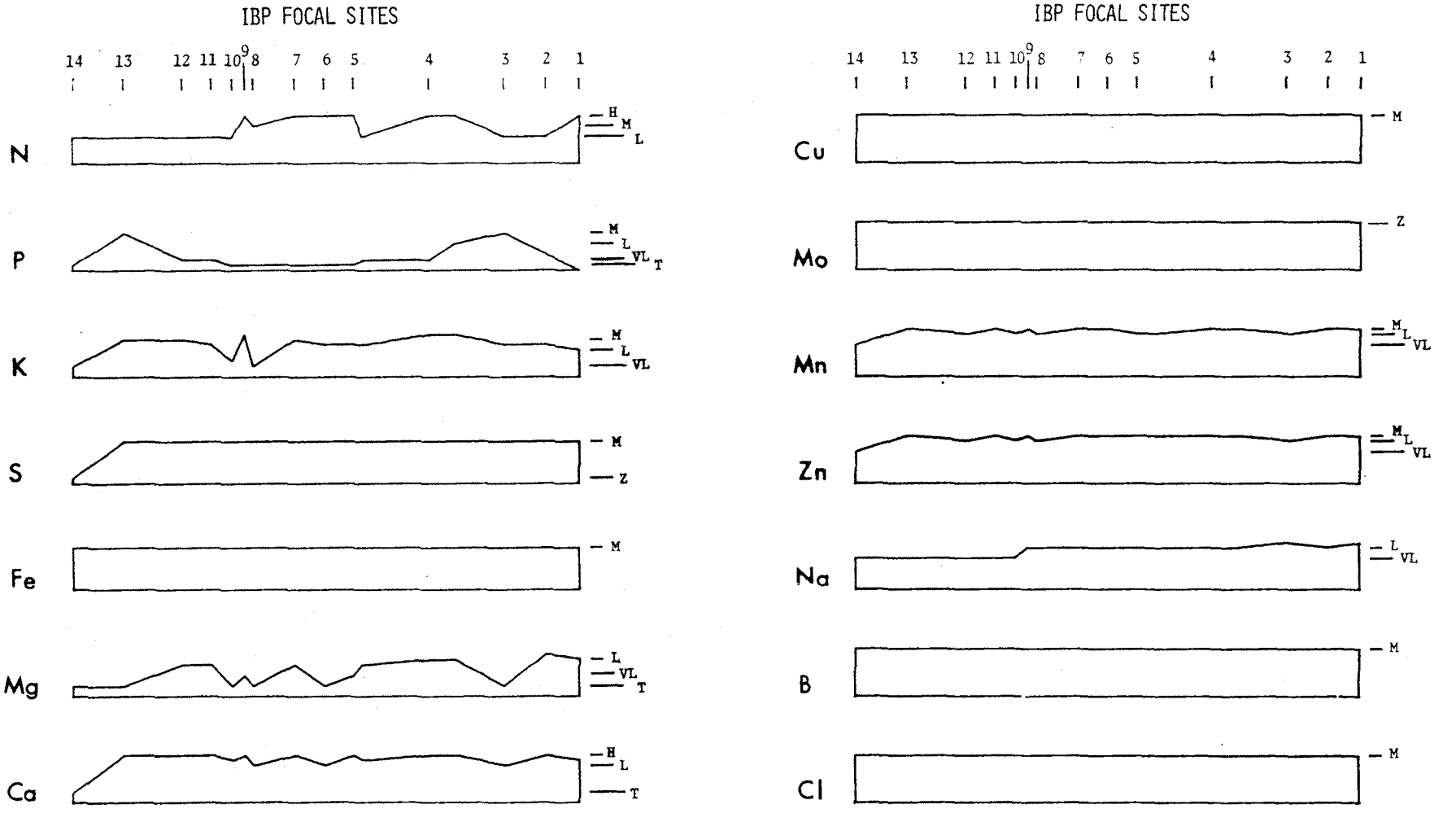


FIG. 6.7. Mineral abundances along the Mauna Loa Transect plotted as values relative to optimal plant growth (as determined for agricultural crops). For positioning of focal sites see the transect profile on Figure 6.8. H = high, M = medium, L = low, VL = very low, T = trace, Z = zero.

6.5-3 Mechanical Factors. The more important mechanical factors can be summarized in three groups: herbivory, ground disturbance, and fire.

Herbivory in the form of cattle grazing was a long-standing influence in the mountain parkland and savanna (Fagerlund 1947) before the area was incorporated into the National Park system in 1927. However, grazing rights were still upheld during the Second World War and up to 1948, when finally all cattle were removed (Apple 1954). This undoubtedly had the pronounced effect of reducing Acacia koa tree communities to only scattered survivors of old-growth trees, as can be observed today on the adjacent ranchland (Cuddihy 1975). Baldwin and Fagerlund (1943) considered cattle grazing the only significant herbivore influence at that time. However, feral goats (Capra hircus L.) roamed the same territory probably a few decades after their introduction by Captain Cook in 1778. Their range of distribution then was undoubtedly wider than that of cattle, since they have been seen throughout the transect from the tree line ecosystem (segment 5 on Fig. 6.2) to open Metrosideros dry forest (segment 10). They stay away only from the rain forest. Their concentration center along the transect is in the mountain parkland (segment 7, Fig. 6.2). However, the control measures exercised by the Park Service are causing a changing pattern of distribution throughout the Park. Their greatest abundance and disturbance effects have been in the coastal lowland section (TR 13). Their number in the montane seasonal section was estimated to be between 1000 and 2000 in 1966 (Mueller-Dombois 1967). In this area they move about in small herds of about 10 to 30 individuals where they feed particularly on the sucker reproduction of Acacia koa. The Park Service stepped up its goat control program in 1960 (Gerdes 1964), when from 1000 to 5000 goats were killed in the entire Park. The effect of this stepped up goat control program became evident in a comparison of air photos taken in 1954 and in 1965. According to these photographs the vegetatively reproducing koa colonies expanded by a rate of 0.5-2.5 m per year into the surrounding grass matrix (Mueller-Dombois 1967). The effect of goats on koa reproduction was subsequently studied in detail in an exclosure at 6200 feet (1890 m) and throughout the mountain parkland at various places (Spatz and Mueller-Dombois 1973). It was found that the goat population did not prevent sucker reproduction, but their browsing effect seemed to produce an abnormally dense stocking of suckers in a haphazard pattern. Where these suckers had a chance to grow in height beyond their browsing reach (at about 1.7 m), the suckers tended to form denser koa stands than one would expect without the mechanical damage caused by goats during the sucker initiation stage. Since 1972

the goat control program has been intensified so koa suckers are now sprouting in the grassland around nearly all koa colonies. However, it is doubtful that the grassland matrix in the parkland will ever disappear under koa because of other mechanical influences.

Ground disturbances from feral pigs (Sus scrofa L.) is a very common mechanical influence throughout the mountain parkland and particularly in the savanna (segment 8, Fig. 6.2). Their effect on the grass cover composition has been studied experimentally (Spatz and Mueller-Dombois TR 15). It was found that pig-rooting favors decidedly the replacement of the dominant native bunchgrass Deschampsia australis by the introduced European weedgrass Holcus lanatus.

A major fire has apparently never occurred through the mountain parkland and savanna since the area has been controlled by the National Park Service. However, at least infrequent fires must have occurred in the past as evidenced by the charcoal bits found in the surface ash soil throughout the area (Mueller-Dombois 1967, Vogl 1969). Charcoal was found at 70 cm soil depth under the kipuka forest (segment 9, Fig. 6.2) and dated as 2,170 $\pm$ 200 years old (Mueller-Dombois and Lamoureux 1967). This indicates that fire has been a long-interval natural perturbation in this transect area, which probably includes segments 7 through 9. Natural fires can be caused by intervening lava flows during volcanic activity.

In spite of the dynamic situation resulting from these mechanical influences, the central area of the transect can be considered relatively stable and in balance with the prevailing climate and substrate. This can be said for two reasons: (1) that a generally similar vegetation (savanna and parkland, although much more disturbed) occurs on the east flank of Mauna Kea (Mueller-Dombois and Krajina 1968), and (2) that the spatial scale of the ecosystems as defined on the profile is wide enough to allow for small area dynamic changes without affecting their overall structure.

6.6 Hypotheses of Species Distribution

We had several initial working hypotheses which involved special consideration of species distributions. One of these was that endemic island birds, insects, and other subsidiary life-forms evolved primarily in adaptation to the community structure-forming dominant native plant species. To test the degree of spatial association of native biota, we sampled along the Mauna Loa Transect, which cuts through the four environmental sections as discussed above.

Another initial working hypothesis was that climatic factors have significant

effects on ecosystem stability. We surmised from general observations that rain forest ecosystems would be more stable than seasonal ones. As an initial index of native ecosystem stability we intended to use the proportions of native and exotic population sizes within organism or life-form groups of an ecosystem, realizing, however, that stability involves persistence over time in the presence of certain disrupting forces or perturbations. Since both rain forest and seasonal environments occur along the Mauna Loa Transect, data from our studies should allow us to test this general hypothesis of ecosystem stability.

Investigations of species distribution problems similar to ours had been conducted in continental ecosystems prior to our study. In order to compare our results with results of the other studies, we adopted the hypotheses proposed by these investigators, with suitable modifications and elaborations.

According to Whittaker (1970), there are currently four hypotheses on species distribution patterns. For clarity, these are here quoted in full as he has presented them (Whittaker 1970:35):

1. Competing species, including dominant plants, exclude one another along sharp boundaries. Other species evolve towards close association with the dominants and toward adaptation for living with one another. There thus develop distinct zones along the gradient, each zone having its own assemblage of species adapted to one another, and giving way at a sharp boundary to another assemblage of species adapted to one another.
2. Competing species exclude one another along sharp boundaries, but do not become organized into groups with parallel distributions.
3. Competition does not, for the most part, result in sharp boundaries between species populations. Evolution of species toward adaptation to one another will, however, result in the appearance of groups of species with similar distributions.
4. Competition does not usually produce sharp boundaries between species populations, and evolution of species in relation to one another does not produce well-defined groups of species with similar distributions. Centers and boundaries of species populations are scattered along the environmental gradient.

All of the four spatial distribution patterns seem possible, although few tests have been made on the hypotheses. Whittaker's studies in continental temperate mountain ecosystems support the last named hypothesis. However, Daubenmire (1966) suggests an altitudinal zonation of dominant tree species in eastern Washington and northern Idaho that supports the first hypothesis.

A slightly different approach has been taken by Terborgh (1971), who studied the altitudinal distribution of bird species on an Andean mountain gradient in Peru through four ecological zones. He suggests three models of altitudinal

distribution. His first model implies that species distributions overlap broadly and vary continuously along an altitudinal gradient in parallel with continuously varying environmental and biological factors. By biological factors he means, for example, tree species or canopy characteristics that provide the food source and shelter of birds. This pattern is the exact equivalent of the one proposed in Whittaker's fourth hypothesis; the implied causes are also the same. Terborgh's second model hypothesizes that distribution limits of species are controlled by competitive exclusion. As the resulting pattern he suggests sharp discontinuities between cogeneric species along the gradient but broadly overlapping ranges of taxonomically unrelated species. This model is similar to Whittaker's second hypothesis. Terborgh's third model suggests that distributional limits are determined by site-factor discontinuities along a gradient. In this case the resulting distribution pattern would be one of zonation of communities with reasonably sharp boundaries. Terborgh uses the term "ecotone" for such boundaries. Except for the underlying reasons, Terborgh's third pattern would be the same as the one proposed in Whittaker's first hypothesis. Whittaker's hypotheses do not consider such a situation, although along any complex gradient, one can expect steep environmental subgradients to occur as a normal phenomenon.

For the reasons suggested in our initial working hypothesis (stated in the first paragraph of this section), we hypothesized that the distribution pattern of the native biota along the Mauna Loa Transect may follow the pattern proposed in the first and/or third hypotheses of Whittaker--that is, evolution toward adaptation to one another resulting in spatially associated species groups. In contrast, we further hypothesized that the introduced biota would follow the distribution pattern suggested in Whittaker's fourth hypothesis.

The fundamental question we are raising has been very clearly stated by Robert H. MacArthur (1972:161):

> A critical question remains: Do different plant species change synchronously, or does each have independent distribution? If they change synchronously, vegetation types are more than a mere convenience; they are real and hence necessary as a subject of study. Whittaker (1969) has spent much of his life investigating this and has shown fairly convincingly for mountains in the United States that plants appear and disappear independently as we go up a mountain. Holdridge might dispute this, for the tropics at least, where he believes plants change synchronously. However, no one has carried out in the tropics a study like those of Whittaker and we must await such a study before we can pass final judgment on whether life zones are real in nature or whether they are the scientist's convenient but arbitrary classifications.

Our study adds two further dimensions to MacArthur's statement: (1) we are concerned not only with plant species but a number of complementary biota, and (2) our gradient is in a tropical island situation, and on a geologically young mountain.

The gradient study has further implications for the relationship of species diversity and community integration. This relationship is usually interpreted for homogeneous or uniformly heterogeneous habitats (e.g. Poore 1964). In the context of uniform habitats, species diversity has been called alpha-diversity by Whittaker (1970). He distinguishes this from beta-diversity, the species diversity along habitat gradients.

Whittaker holds that the highest degree of integration is accomplished by a high beta-diversity. High beta-diversity implies accommodation of a large number of species with restricted distributions along a given environmental gradient as opposed to a few wide-ranging species on the same gradient. Low beta-diversity appears to be a characteristic along altitudinal gradients on oceanic islands, at least in Hawaii. In the tropics, this is a pecularity only for islands. Whether this also means poor integration, needs further examination. An increase of beta-diversity through exotic species invasions appears to show the opposite, namely a decrease in integration.

6.7 Field Sampling Design

The sampling for different organism groups requires techniques that are more or less specific for each major group. These will be discussed in the next chapter at the appropriate places. Here we will present only the sampling aspects relating to the overall design.

Some of the sampling techniques required more effort than others. Therefore, it was expected that the number of sampling locations would vary between investigators. For this reason, some degree of stratification became necessary that would yield a relatively high sampling efficiency. This was done in several ways: (a) by utilizing the previously defined transect segments as a reference framework for the establishment of a certain minimum number of focal or coordinated sampling sites, and (b) by stratifying the vegetation within focal sites into life-form communities.

During an IBP field meeting in August 1972, we decided as a team that each transect investigator would sample his organism group in a minimum of 14 identical locations along the Mauna Loa Transect. The common locations were those where a

majority of the investigators had already sampled prior to this decision. The 14 focal IBP transect sites are briefly described in Table 6.1. Figure 6.8 portrays the locations of these focal sites with their altitudinal limits on a profile diagram that corresponds in scale to the one shown on Figure 6.2.

The originally contemplated sampling layout was to have a focal site rather systematically distributed at every 1000-foot level (~300 m) of altitude. This resulted in the following seven stations:

Elevational level (feet)	Type of Vegetation	Final IBP Site Number
4000 (1220 m)	Closed rain forest	1
5000	Mountain parkland	5
6000	Mountain parkland	8
7000	Subalpine scrub-forest	10
8000	Near tree line	12
9000	Sparse alpine scrub	13
10000 (3050 m)	Upper limit of sparse alpine scrub	14

Then, seven additional sites were established to intensify the sampling network and to include a few more site variations. Three additional sites were established at the 4000-foot level to cover the major site variations between the closed rain forest and the mountain parkland. These are sites 2 (open Metrosideros rain forest), 3 (open Metrosideros dry forest), and 4 (savanna) as shown in Figure 6.2. Four other sites were established at the middle section of the transect: two additional ones in the mountain parkland (sites 6 and 7), one at the border of the mountain parkland with the subalpine scrub-forest (site 9), and one at the border between the latter and the tree line ecosystem (site 11). Note that three sites are ecotonal (sites 9, 11, and 14) in relation to the previously defined transect segments or ecosystem types. It was felt that this would add interest for the subsequent analysis of species distributions along this mountain gradient. A few investigators also sampled in between the focal sites. This was particularly true for the vascular plant analysis which was more or less continuous with at least three samples for every 500-foot (~150 m) interval (see Chapter 7.1-1).

A further stratification within focal sites was considered desirable because of the different behavioral scale of our organism groups as explained in Chapter

TABLE 6.1. Focal IBP sites on Mauna Loa Transect. See the transect profile, Figure 6.2, for an elaboration of the site characteristics.

IBP site no.	Location and elevation	Vegetation	Transect segment
1	Thurston Lava Tube 3920 ft (1195 m)	Closed Metrosideros-Cibotium (ohia-tree fern) forest	12
2	Sulphur Bank 4000 ft (1220 m)	Open Metrosideros-Gleichenia (ohia-matted fern) forest	11
3	Tree Molds area 4000 ft (1220 m)	Open Metrosideros-native shrub-lichen forest	10
4	Kipuka Ki near climatic station, 4200 ft (1280 m)	Acacia koa-Sapindus savanna	8
5	Power Line Trail 4920 ft (1500 m)	Mt. parkland ecosystem, Acacia koa colony	7
6	IBP Climatic Station 5250 ft (1600 m)	Mt. parkland ecosystem, Acacia koa colony	7
7	Keamoku Flow, just above 5650 ft (1720 m)	Mt. parkland ecosystem, Acacia koa colony	7
8	Above Goat Exclosure 6200 ft (1890 m)	Mt. parkland ecosystem, Acacia koa colony	7
9	End of Strip Road 6700 ft (2040 m)	Mt. parkland ecosystem, Acacia koa colony	7 to 6 transition
10	7000-foot level (2130 m)	Open Metrosideros scrub-forest (scrub with scattered trees)	6
11	7500-foot level (2290 m)	Open Metrosideros scrub-forest (scrub with scattered trees)	6 to 5 transition
12	8000-foot level (2440 m)	Metrosideros tree line ecosystem (open scrub with scattered trees)	5
13	9000-foot level (2745 m)	Vaccinium-Styphelia low-scrub desert (very sparse scrub)	3
14	10000-foot level (3050 m) Puu Ulaula area	Vaccinium-Styphelia low-scrub desert (very sparse scrub)	3 to 2 transition

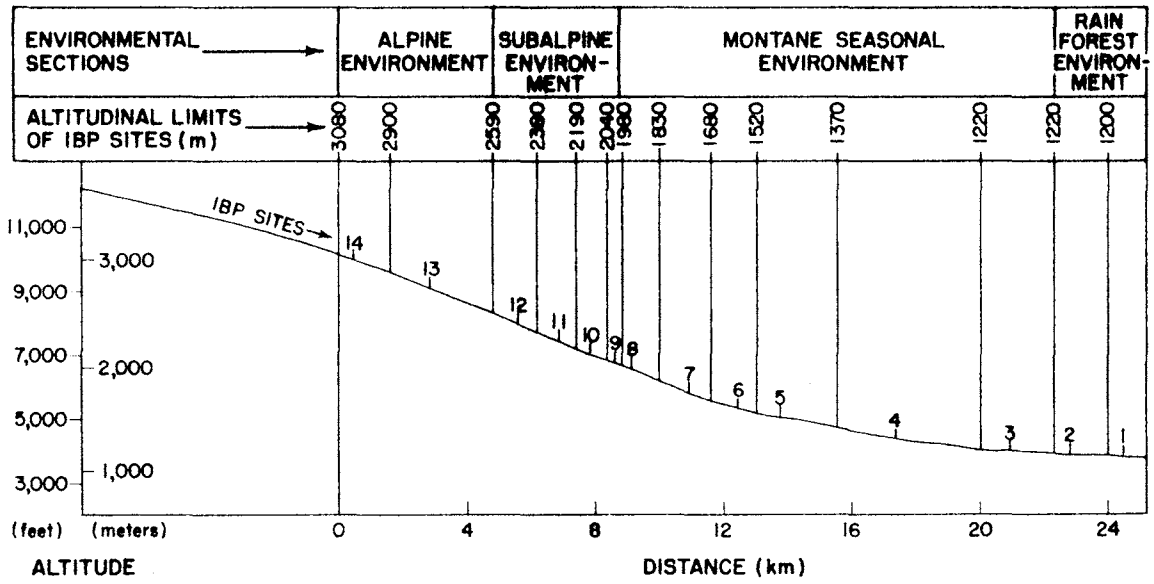


FIG. 6.8. Profile diagram of Mauna Loa Transect showing locations and altitudinal limits of the 14 IBP focal sites in relation to the four environmental sections (as mapped on Fig. 6.1).

4.3. This relates to an easily recognizable quantitative classification of plant communities on a finer level of structure. Three life-form communities were defined for this purpose as follows:

(1) Tree community, defined as an aggregation of woody plants that form a "closed" canopy (meaning at least 60% ground cover) covering at least 60 m^2 ground surface (i.e. 2 or more trees), and that have their maximum crown biomass at 5 m height or taller.

(2) Shrub community, defined as a grouping of woody plants having their maximum crown biomass between 0.2 and 5 m height. Over 50% of the shoot biomass must be of the shrub life-form (i.e. woody plants). No ground cover limit was assigned. Therefore, shrubs can be very scattered (e.g. 1 per 100 m^2), but they must always be present in greater quantity than herbaceous plants.

(3) Grass community, defined as a grouping of herbaceous plants among which more than 50% of the shoot biomass must be of the grass life-form. No ground cover limit was assigned. Therefore, grass communities can also be very sparse or desertlike, but herbaceous life-forms must predominate.

The three quantitative structural definitions match closely what most field biologists would intuitively classify as tree, shrub, and grass communities, respectively.

The site comparison table (Table 6.2) presents a summary by IBP focal sites of the sample locations and numbers as used by individual investigators. Further details of sampling locations are given, where appropriate, in the next chapter relating to the discussion of the individual organism groups.

6.8 Data Analysis

When investigating species distributions, it is necessary to have an analytical methodology to objectively demonstrate the distribution patterns. Whittaker (1967) has employed two techniques: he used a sample stand ordination that he called the double weighted-average technique; he further performed species ordinations by drawing plots of species distributions in the form of his well-known bell-shaped curves along the gradients that he investigated.

We adopted a similar approach here, although it is based on different analytical techniques. We feel that the techniques which we have adopted will allow us to make more discriminatory interpretations of our data.

Several criteria were employed in our selection of analysis techniques. It

TABLE 6.2. General site comparisons. The numbers for each investigator refer to his site sampling scheme. Sampling sites falling on the transect are aggregated at the nearest IBP focal sites. Specific qualifications are given in the chapters discussing each investigator's results.

			INVESTIGATORS AND ORGANISM GROUPS															
IBP FOCAL SITE	SITE NAME	ELEVATION FEET (M)	BAKER, leaf and litter fungi	BEARDSLEY, sap-sucking insects	CONANT, birds	DOTY, soil algae	GAGNÉ, canopy insects	HARDY, litter insects	LAMOUREUX, tree phenology	MITCHELL, blossom-feeding insects	MUELLER-DOMBOIS, SPATZ vascular plants	NISHIDA, tree insects	PAIK, Drosophila	RADOVSKY, soil arthropods, ectoparasites	SAMUELSON, wood and bark beetles	STEFFAN, Sciaridae	STONER, soil fungi	TOMICH, rodents
1	THURSTON	3920(1190)			1	18	1	3	7		1	2		18	✓	1	2	6
2	SULPHUR BANK	4000(1220)					2	4	6		2	3	1		✓		3	5,16
3	TREE MOLDS	4000(1220)		3	3	11,12	3	5	5	3	3		2	10,11,12	✓	3	4	
4	KIPUKA KI	4200(1280)	4		4	8,9,16	4	6,7			4		3	8,9,16	✓	4	5,6	4,15
5	POWERLINE	4920(1500)			5	20		8			5			20	✓	5	7,8	3
6	CLIMATE STA	5250(1600)	3			6	6	9	3		6		4	6,7	✓	6	9	
7	KEAMOKU	5650(1720)		7	7	25				7	7		5		✓	7	10	
8	GOAT EXCL	6200(1890)						10	2		8		6	5	✓	8	11	2
9	END STRIP RD	6650(2030)		9	9	4	9	11	1	9	9		7	4	✓	9	12	
10	7000'	7000(2130)	2	10		3	10	12		10	10	4	8	3	✓	10	13	1
11	7500'	7500(2290)				29		13			11		9	2	✓	11	14	
12	8000'	8000(2440)	1	12	12	1	12	14,15		12	12		10	1	✓	12	15	10,13
13	9000'	9000(2740)				31		16,17			13				✓		16	11,12
14	10000'	10000(3050)				33		18			14				✓		17	14

was most important that the techniques be able to handle the type and quantity of data collected in the investigations. This includes both quantitative and qualitative data. The proven usefulness of the techniques was considered to be important; the introduction of new types of analysis was avoided because it could possibly compound the interpretation problems. The volume of the data to be analyzed and the need for uniformity in the analysis procedures required that we utilize computer analysis techniques. Where possible, programs were obtained which were already operational. In selecting these programs the ease of data preparation, the program capacity, and the ease of installation on the local computer were evaluated. When necessary, additional programs were written to supplement the series of analysis programs.

The series of analytical programs has proven to be quite flexible and easy to use. The data are all stored in a common machine-readable format. These data are then processed with a program which selects the relevés* to be analyzed and, based on the input of a few control parameters, produces a data set which is formatted for the various analysis programs. This approach of using a series of programs linked by data sets has allowed us to mix the use of programming languages so that the features of each may be exploited.

Since an understanding of each of these techniques is important for the interpretation of the remainder of this part, each one will be described and demonstrated with an example.

6.8-1 Sample Ordination by Dendrograph Technique. The analysis objective for sample ordination was to determine the similarity pattern among the various sample locations along the transect by subjecting the total species content of each spatial sample to a similarity test. Whittaker's (1967) double weighted-average technique resulted in scatter diagrams of sample stands not unlike those produced by the Wisconsin ordination technique (Bray and Curtis 1957, Beals 1960, Newsome and Dix 1968). The two techniques differ very much in detail, but their objective is the same--namely, to demonstrate sample similarities geometrically. The geometric distance among samples then allows one to recognize the presence or absence of groups or clusters of similar samples.

During the past decade dendrograms have become more widely applied in multivariate analyses of this sort (Frenkel and Harrison 1974, Orloci 1975). Like the Wisconsin ordination technique, dendrograms are a diagrammatic tool for displaying the content of a similarity matrix (Mueller-Dombois and Ellenberg 1974).

*Relevé is the French word for abstract. We use this word throughout this text as the equivalent of community sample, i.e. a sample containing usually more than one species.

The dendrogram technique generates clusters of samples at various degrees of similarity. However, the recognition of ecologically meaningful clusters presents problems of interpretation similar to those in geometric methods. Cluster interpretation will be discussed below after introducing the dendrogram technique used for our analysis here.

For our purposes we used the dendrograph technique of McCammon (1968, McCammon and Wenniger 1970) because of its flexibility and tested usefulness.

A dendrograph differs from the usual dendrogram in that the between-group distances or similarities are also calculated and shown diagrammatically by scaling the distances along the x-axis. However, the main feature of any dendrogram or dendrograph is the within-group distances or similarities which are shown along the y-axis of each dendrogram or dendrograph.

Figure 6.9 is a dendrograph comprised of 48 community samples or relevés (36 tree and 12 shrub relevés) that describe the 14 IBP focal sites. Individual relevé numbers are shown on the left-hand side (the two rows of numbers that are not blocked out) along the x-axis of the dendrograph. Next to the individual relevé numbers (along the x-axis) are the corresponding IBP focal site numbers, which are here blocked out for clarification. The y-axis (top and bottom on the diagram) gives a similarity scale from high (100%) at left to low at right. The asterisks along the y-axis occur at 10% similarity intervals.

The relevé groups or clusters are indicated by horizontal lines connecting the various relevés. The distance of this horizontal line from the y-origin (at 100% similarity) shows the within-group similarities. Since the clusters are hierarchically arranged, it is important to evaluate both the number of relevés which have been grouped and the similarity of the group. Ecologically meaningful groupings are not established automatically. They have to be identified. But before we proceed with the ecological interpretation, we will briefly describe how the dendrograph was constructed.

The general procedure employed in determining the relevé similarities is illustrated below. A description of the other similarity indices is given in Mueller-Dombois and Ellenberg (1974).

First, a matrix of similarity indices or community coefficients was calculated using Motyka's quantitative modification of Sørensen's index. This index reads as follows:

$$IS = \frac{2w}{A + B} \times 100$$

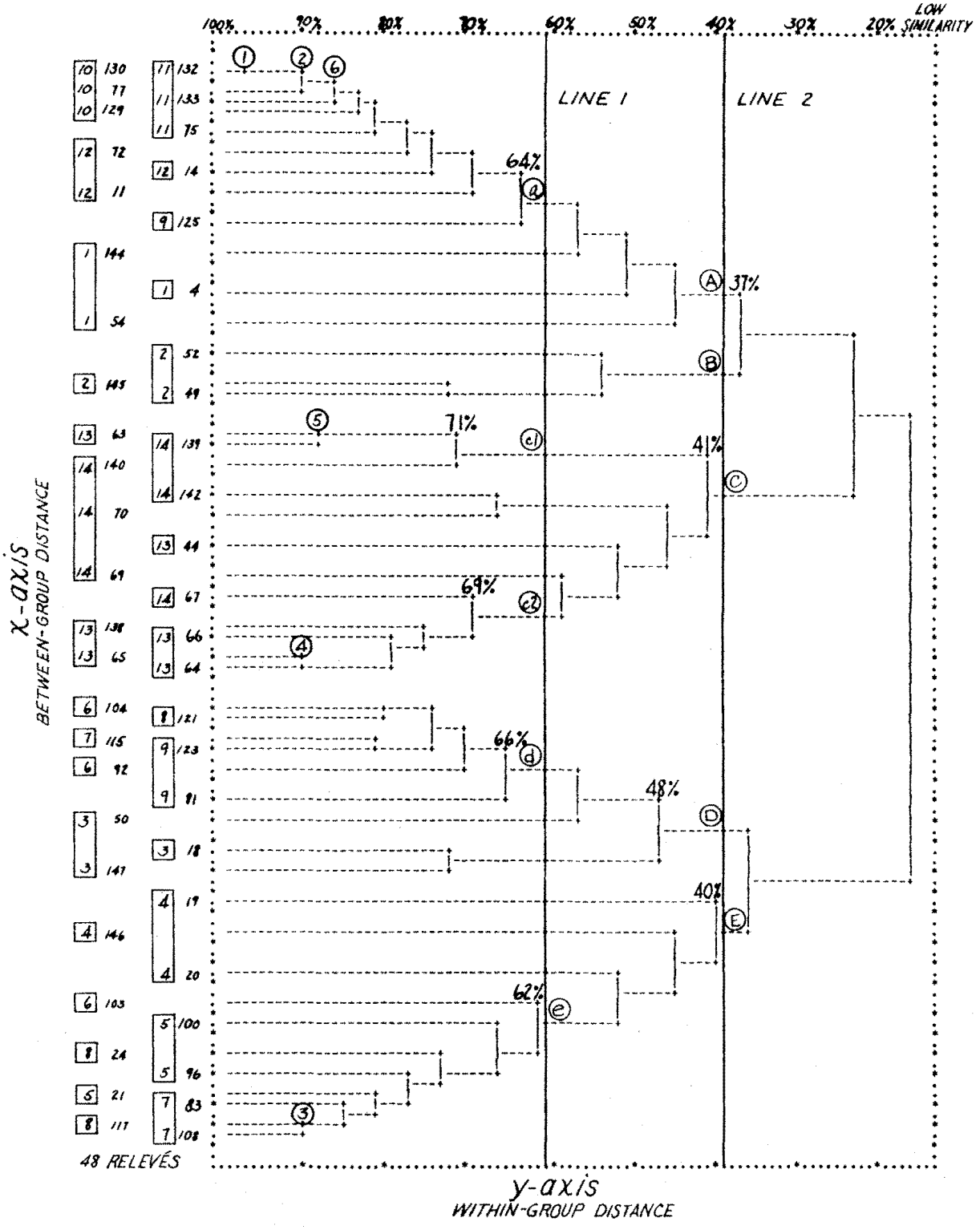


FIG. 6.9. Dendrograph based on 48 vegetation samples (36 tree relevés plus 12 alpine shrub relevés) compared with the quantitative Sørensen index of similarity. Blocked out numbers are IBP site numbers [1 - 14]. Numbers not blocked out are relevé numbers.

where IS = Index of similarity

A = Sum of quantitative values of all species in relevé A

B = Sum of quantitative values of all species in relevé B

w = Sum of the smaller of the two quantitative values of the species that are common to relevés A and B

The number of comparisons involved are n(n-1)/2, which for 48 relevés comes to 1128 IS values. Table 6.3 shows a part of the computer-derived similarity matrix. The remaining part was omitted to save space and because the procedure can be explained from this restricted section of the matrix.

The second major step in the analysis is the construction of the dendrograph. The dendrograph program of McCammon (1968) is based entirely on the similarity matrix, so that the dendrograph is merely a mathematically derived diagrammatic display of the content of a similarity matrix. Among various cluster analysis techniques available (Sneath and Sokal 1973, Orloci 1975), McCammon's program can be defined as an agglomerative, centroid, unweighted pair-group method. The procedure is explained briefly in five steps as follows:

1. The computer is programmed to convert all percent IS values into metric distance values by the arc cosine transformation. This transformation is done so that the similarity values can be averaged correctly in subsequent computations. This avoids the problem of averaging percentage values. The arc cosine transformation changes high similarity values into low distance values and vice versa (e.g. IS 90% = arcos 0.451 and IS 10% = arcos 1.471).

2. The computer then searches the matrix for the lowest arc cosine value (which corresponds to the highest IS value). By detecting this value it has located the two relevés that are most similar in their quantitative species content. In our example this pair is comprised of relevés 130 and 132. The two relevés share an IS value of 97.1% (see Table 6.3). This value is plotted as output cluster (1) on the dendrograph (Fig. 6.9).

3. The computer then averages all distance values of the two relevés (130 and 132). This implies a reduction of the two columns in the similarity matrix (under relevés 130 and 132) to one and a reduction of n - 1 = 47 values (for a second matrix not shown here).

4. The computer then searches the entire matrix again for the lowest distance value. This value may be found among the previously calculated ones, or it may be among the 47 new average values. In our example it was among the new average values.

TABLE 6.3. Part of a similarity matrix*. Relevé numbers are shown on left side and at top; the matrix values are similarity indices in percent based on the quantitative modification of Sørensen's index. More explanation in text.

RELEVÉ	117	121	123	125	129	130	132	133	138	139	140	142	144	145	146	147
52	6.9	6.8	8.2	10.7	27.7	27.2	26.3	24.7	0.1	0.1	0.3	0.0	23.5	34.5	2.4	31.0
54	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	29.4	0.0	1.4	0.0
63	0.4	0.0	4.6	22.2	19.9	22.5	23.3	9.5	46.2	87.9	58.8	24.0	0.0	0.0	0.0	0.3
64	0.5	0.0	4.8	13.3	8.3	9.8	9.9	14.0	66.7	37.1	37.6	48.8	0.0	0.0	0.0	3.3
65	0.7	0.0	4.9	13.6	8.5	10.0	10.3	9.8	76.1	40.8	38.5	27.9	0.0	0.0	0.0	3.4
66	0.6	0.0	0.9	5.7	5.0	6.1	6.0	6.1	66.7	27.6	32.2	39.7	0.0	0.0	0.0	0.3
67	0.0	0.0	0.2	5.3	4.6	5.5	5.6	5.9	42.1	29.8	17.8	50.5	0.0	0.0	0.0	0.0
69	0.0	0.0	0.0	0.2	0.2	0.2	0.2	0.2	1.9	1.3	0.6	2.6	0.0	0.0	0.0	0.0
70	0.0	0.0	0.4	5.2	4.9	5.5	5.6	5.9	50.5	33.3	18.6	66.7	0.0	0.0	0.0	0.0
72	3.0	2.5	5.5	16.1	76.8	66.2	68.0	59.1	15.0	24.3	29.5	5.4	28.0	30.7	0.1	33.5
75	3.4	3.0	17.4	31.6	73.2	78.3	77.7	64.9	12.4	28.2	43.5	6.2	30.4	33.6	2.1	38.7
77	3.1	2.7	14.2	33.0	78.9	84.2	86.8	74.4	11.7	26.8	41.6	5.8	29.7	32.7	0.2	46.9
81	30.5	71.7	50.4	23.8	7.7	8.3	5.8	8.2	5.6	4.9	4.8	5.3	0.0	0.0	3.8	34.1
83	83.9	53.6	55.9	26.6	6.5	6.9	4.7	6.9	0.3	0.0	0.3	0.0	0.0	0.0	10.0	21.2
92	57.1	65.3	68.0	28.8	5.3	5.6	3.0	5.6	0.4	0.0	0.3	0.0	0.1	0.0	11.3	13.9
96	74.2	40.6	43.0	25.1	4.7	5.0	2.6	2.8	0.0	0.0	0.0	0.0	0.2	0.0	18.1	19.4
100	40.7	41.6	44.1	29.0	4.8	5.1	2.6	5.0	0.4	0.0	0.3	0.0	0.3	0.0	17.7	21.0
103	38.0	39.2	48.7	31.4	4.6	4.9	2.5	2.5	0.0	0.0	0.0	0.0	0.2	0.0	23.1	18.9
104	56.4	80.7	59.6	20.6	14.6	15.6	13.3	15.8	0.0	0.0	0.0	0.0	0.0	0.0	11.1	48.9
108	90.0	64.4	64.7	24.1	2.8	3.0	2.7	5.0	0.5	0.2	0.4	0.0	0.0	0.0	8.9	16.8
115	65.3	81.1	81.5	28.7	2.9	3.1	3.0	5.7	0.4	0.0	0.3	0.0	0.0	0.0	9.4	20.2
117		61.7	62.1	23.4	2.9	3.2	3.0	5.3	0.6	0.2	0.5	0.0	0.0	0.0	7.5	17.8
121			77.3	24.9	2.5	2.7	2.6	5.1	0.0	0.0	0.0	0.0	0.0	0.0	9.2	36.6
123				45.0	14.4	15.5	13.2	15.3	5.0	4.4	15.9	0.0	0.0	0.0	16.2	19.3
125					35.4	37.9	36.2	28.3	10.0	22.3	31.6	4.7	0.0	0.0	21.7	21.3
129						81.7	81.3	70.7	8.8	20.4	32.6	4.4	26.1	28.4	1.9	41.2
130							97.1	85.6	10.3	23.4	36.7	5.4	27.4	30.0	2.0	43.4
132								85.3	10.6	24.2	37.5	5.0	28.0	30.7	0.1	42.1
133									10.2	9.7	24.9	9.9	27.8	30.5	0.1	41.8
138										50.2	43.2	38.5	0.0	0.0	0.0	0.3
139											63.5	29.2	0.0	0.0	0.0	0.1
140												17.3	0.0	0.0	0.0	3.3
142													0.0	0.0	0.0	0.0
144														25.2	0.5	24.4
145															0.1	26.0
146																14.8
147																

* The complete matrix contains $\frac{n \cdot (n-1)}{2} = \frac{48 \cdot (47)}{2} = 1128$ values. The complete set of similarity indices is not shown here because the omitted values are not needed for the explanation of the dendrograph technique.

This is indicated by output cluster (2) on the dendrograph (Fig. 6.9) which joins relevé 77 at 90.3% within-group similarity to the already established first cluster formed by relevés 130 and 132.

5. The computer then calculates a new set of average values by combining relevé 77 with the former average values of relevés 130 and 132. As a result the matrix is reduced once more. In our example, the third highest IS value (or the third shortest distance value) was located among the originally calculated values on Table 6.3. It is the IS value of 90% similarity shared by relevés 117 and 108. This relevé pair was plotted as output cluster (3) on the dendrograph (Fig. 6.9).

The computation cycles are repeated in this way until all relevés are clustered. The dendrograph is not printed until the entire network sequence of output clusters is established. All numerical values for the output clusters and their sequence are shown on Table 6.4. However, the cosine values for within- and between-group distances were not reconverted into percentage similarity values. The percent values have been subsequently added for the first six output clusters. Their sequence can be found on the dendrograph (Fig. 6.9) by moving a straightedge from left (high within-group similarity) to right (low similarity).

For an ecological interpretation of the dendrograph it is important to locate the most meaningful clusters. If ecologically meaningful clusters or relevé groupings occur at all, they may be expected to be in the mid-range of similarity. This is because at high within-group similarities all relevés or community samples are unique, while at low similarities they are all joined into one large all-inclusive group or cluster. On Figure 6.9, the latter all-inclusive cluster occurs at 16% within-group similarity. In our example this cluster lumps all four environmental sections of the Mauna Loa Transect together, i.e. the alpine, subalpine, montane seasonal, and montane rain forest sections.

6.8-1.1 Rules for Identifying the Major Dendrograph Clusters. At this point one can detect ecologically meaningful clusters in two ways: (a) deductively, by identifying those clusters that best define various predetermined transect segments or ecosystem types, or (b) inductively, by establishing certain arbitrary rules that automatically isolate a number of clusters in the mid-range of within-group similarity.

Since we are aiming at objectively defining transect zones by a uniform procedure applicable to several different organism groups, we opted for the second approach. For this purpose we established arbitrary cutoff lines (which can be

TABLE 6.4. Computer-derived output clusters with corresponding within- and between-group arc cosine distances. These values, converted into percentages*, are the basic values used for plotting the dendrograph (Fig. 6.9).

RELEVÉ	FINAL RESULTS OUTPUT CLUSTER		WITHIN GROUP	BETWEEN GROUP	
130	①	97.1%	0.2410	0.2410	97.1%
132	②	90.3%	0.4435	0.5448	85.5%
77	⑥	86.5%	0.5256	0.6078	82.1%
133	8		0.5837	0.6707	
129	10		0.6286	0.7185	
75	15		0.6888	0.8394	
72	17		0.7320	0.8617	
14	24		0.8030	1.0513	
11	29		0.8880	1.2281	
125	32		0.9712	1.3454	
144	37		1.0361	1.3609	
4	41		1.1087	1.5080	
54	44		1.1879	1.3603	
52	34		1.0041	1.1246	
145	21		0.7630	0.7630	
49	46		1.3358	1.4936	
63	⑤	87.9%	0.4972	0.4972	87.9%
139	22		0.7744	0.9129	
140	42		1.1456	1.2598	
142	26		0.8410	0.8410	
70	39		1.0909	1.1975	
44	36		1.0318	1.2627	
69	31		0.9395	1.2008	
67					

RELEVÉ	FINAL RESULTS OUTPUT CLUSTER		WITHIN GROUP	BETWEEN GROUP	
138	25		0.8089	0.9391	
66	16		0.7220	0.7960	
65	13		0.6480	0.7465	
64	④	90.0%	0.4510	0.4510	90.0%
104	47		1.4079	1.5250	
121	12		0.6321	0.6321	
115	18		0.7359	0.7913	
123	9		0.5181	0.6181	
92	23		0.7858	0.8606	
81	28		0.8600	1.0084	
50	33		0.9734	1.2567	
18	38		1.0957	1.2773	
147	20		0.7628	0.7628	
19	45		1.2066	1.2750	
146	43		1.1625	1.4224	
20	40		1.1048	1.4212	
103	35		1.0257	1.4270	
100	30		0.9110	1.1012	
24	27		0.8476	1.1139	
96	19		0.7411	0.8512	
21	14		0.6861	0.7718	
83	11		0.6290	0.7058	
117	7		0.5521	0.6029	
108	③	90.0%	0.4506	0.4506	90.0%

* In this table carried through only for output clusters 1 to 5.

used as rules) that permit objective identification of dendrograph clusters in the mid-range of within-group similarity. A major cluster should be defined from the number of replicate samples. For example, in this case where a minimum of 3 replicate samples was used to describe each of the 14 IBP sites, a major cluster was defined as a grouping of at least 3 relevés.

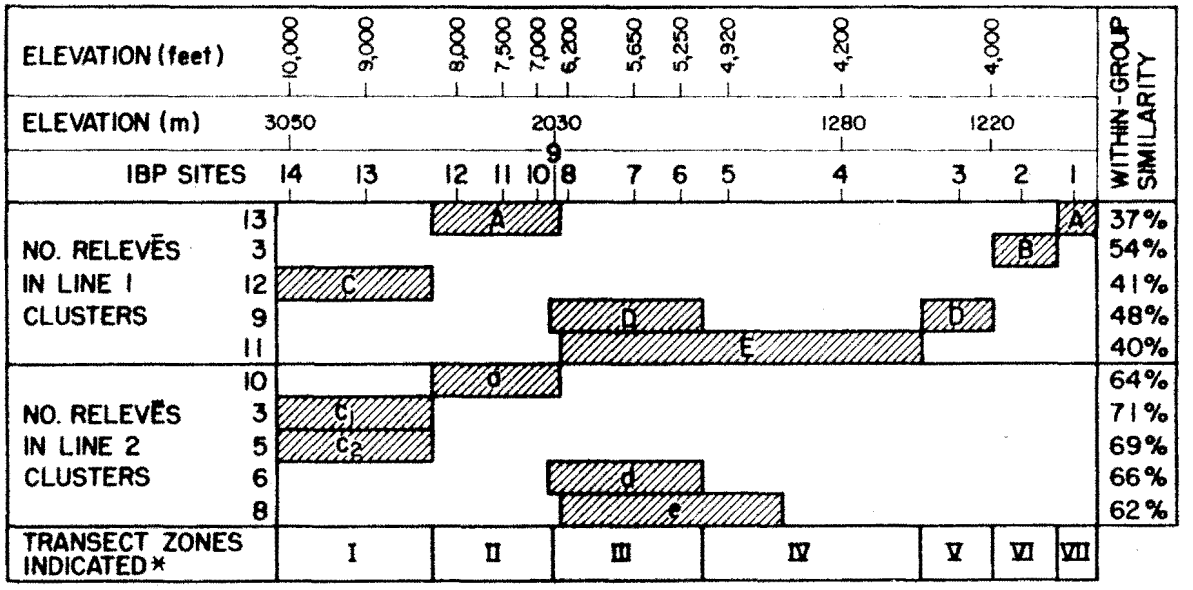
The two cutoff lines shown on the dendrograph (Fig. 6.9) are defined as follows:

Line 1 isolates the major clusters by minimizing the number of single clusters. In case of ambiguity the number of major clusters takes precedence over the single clusters.

Line 2 isolates any number of major clusters where the number of single clusters is just under 25%.

In our example line 1 identifies five major clusters (A, B, C, D, and E) at a level of within-group similarity ranging from 37% to 48% as shown on Figure 6.9. Line 2 likewise identifies 5 major clusters (a, c1, c2, d, and e), which here can be called higher-similarity subclusters occurring at a within-group similarity range of 62% to 71%. These latter subclusters, which are portions of the major clusters, are relatively more homogeneous.

6.8-1.2 Transfer of Dendrograph Clusters to Zonation Diagram (Fig. 6.10). The 10 dendrograph clusters which were identified by the two previously defined cutoff lines must now be interpreted ecologically. For this purpose their major information content was transferred into what may be called a zonation diagram (Fig. 6.10). From this it can be seen that cluster A combines IBP site 1 (the closed rain forest) with IBP sites 9 through 12 (extending from the upper limit of the mountain parkland through the subalpine scrub forest to, and including, the tree line ecosystem). This line 1 cluster, which combines 13 relevés at 37% within-group similarity, is thus lumping very unlike units into one group. At line 2 the rain forest is split off and subcluster 'a' represents a more homogeneous segment that combines only the tree line ecosystem, subalpine forest with the upper limit of the mountain parkland at the higher within-group similarity of 64%. The meaning of each cluster is easily read from Figure 6.10. For example, cluster B defines the open montane rain forest, cluster C defines the alpine section (with IBP sites 13 and 14), and cluster D defines a rather heterogeneous combination of upper mountain parkland and open seasonal Metrosideros forest (IBP site 3). Again at the second cutoff line, the subcluster d combines



*based on at least two cluster limits

I = Sparse alpine scrub

II = Open subalpine scrub-forest

III = Mountain parkland excluding site 5

IV = Savanna including site 5 of mountain parkland

V = Open Metrosideros dry forest

VI = Open Metrosideros rain forest

VII = Closed Metrosideros rain forest

FIG. 6.10. Zonation diagram: altitudinal distribution of dendrograph clusters formed from 48 vegetation samples (36 tree relevés plus 12 alpine shrub relevés; 169 species) by quantitative Sørensen Index.

only the upper mountain parkland relevés, while the montane seasonal forest is split off. Cluster E combines the mountain parkland with the savanna.

The clusters as defined by the two cutoff lines, therefore, indicate homogeneous zones at different levels of within-group similarity. The question then arises as to what zonal limits are most strongly indicated by the samples, Here again a general ruling has been adopted which can be applied to other sample sets as well. We draw a boundary where at least two cluster limits occur on the zonation diagram. This we feel provides a minimum standard for a "strong" zonal boundary. The resulting transect zones are shown and defined at the bottom of the zonation diagram (Fig. 6.10). It is of interest to note that the boundary of the savanna has been moved up to about 5000 feet (1520 m) by the sample data and the rules imposed on them. The predetermined boundary was set at 4500 feet (1370 m). However, in earlier publications (Mueller-Dombois 1966, Mueller-Dombois and Krajina 1968), the same boundary was also set at 1520 m, which indicates that the mountain parkland-savanna boundary is a very gradual or transitory one.

The clusters can be investigated further as to the species that are particularly responsible for the sample clusters. However, this information is obtained much more easily from the two-way synthesis technique that will be discussed next.

6.8-2 Species Ordination by Two-Way Synthesis Table Technique. After determining the community-sample pattern, the next analysis objective was (as in Whittaker's gradient analysis model) to extract the species distribution trends from our sample sets. To do this we adopted the Ceska-Roemer (1971) program because of its unique flexibilities. This program is a close computer simulation of the Braun-Blanquet synthesis table technique (Mueller-Dombois and Ellenberg 1974: Chap. 9).

Both the dendrograph and two-way synthesis table start their analysis from the same raw data table. In this table each row represents a species and each column represents a relevé or sample site. Within the table, the occurrence of a species in a relevé is entered as its cover, frequency, abundance, or simply presence (depending on the organism being studied). An empty table cell indicates the absence of a species from a relevé.

In the previously discussed dendrograph technique, the columns of the raw data table were intercompared, producing a similarity matrix. Such an analysis has been referred to as Q-technique in numerical taxonomy (Cattell 1966, Sneath and Sokal

1973).

In our second objective, we are particularly interested in comparisons between the species, that is, in an analysis of the between-row similarities and differences. This type of analysis is known as R-technique. The Ceska-Roemer program (similar to the original Braun-Blanquet method) is unique in that it performs both a Q- and an R-type analysis on the data set. For this reason, the program can be called a two-way table technique (Greig-Smith 1964).

The primary emphasis in this type of analysis is the identification of groups of species which have similar distribution ranges. The distribution of these groups may then be used to identify transect zones. Since this is an independent form of analysis (with quite different assumptions), zones established in this analysis may be compared to those from the dendrograph analysis. In addition, the Ceska-Roemer program isolates the species responsible for any emerging relevé group or cluster. Moreover, it performs a distribution analysis of the species throughout a given set of samples or relevés with regard to the species spatial limits and spatial parallels (i.e. association of occurrences).

The essential features of the two-way table program will be discussed next.

6.8-2.1 Analysis of Species with Restricted Distributions. In contrast to the previously discussed dendrograph technique, the two-way table technique is programmed to reject at the beginning those species that are present in all or nearly all relevés. The reason for this is that these omnipresent species do not contribute any information to the differentiation of the zones. The species rejected at the start of the analysis are all those that are present in 66% or more of the relevés under comparison. This is an arbitrarily set limit that conforms to a general norm used in phytosociological work.

The remaining species have limited distribution ranges. The following two sections discuss the procedures which are used to identify groups of associated relevés and the sets of species which characterize them.

6.8-2.2 Definition of Associated Species Groups. The analysis procedure involves the identification of groups of species which are similar because of the pattern of their distributions. The primary difficulty comes, however, in providing a precise definition of similarity in species distributions. The general concept of species distributions is quite clear. We also know that, even in restricted areas, species rarely coincide exactly in their distributions. Two species, however, may

both occur at a majority of the sites sampled along their range. At a few sites one of these species may occur in the absence of the other. If these two species occur at the same sites most of the time, these species have a coincident range (over the common sites), and are thereby associated.

So far we have talked only about comparing two species. The next step is to search for more species that may be considered associated. Some new species may have distributions nearly coincident with the distributions of the original species in the group; but the new species may not be present at a few of the sites common to the first two species. These new species may also occur at a few sites other than the common sites. Thus, as species which characterize the associated group of species are added, two types of distribution exceptions may be found. One of these is the occurrence of a species at a site outside the group of sites. The other is the absence of a species from sites common to the group. The precise thresholds that we establish for these two types of exceptions controls the way species are associated in the group selection process.

In the Ceska-Roemer program, the use of threshold values for species selections is controlled in RuleI: a species is recognized as associated with a group if it occurs in at least X% of the sites or relevés of the group and is not present in more than Y% of the sites outside this group. The actual percentage values used for X and Y can be changed as an option in the program. When X is 50% and Y is 10%, it means that associated species are all those that occur together in 50 to 100% of the sites of the group and in not more than 10% of the sites outside this group. This is known as the 50/10 option, which has been applied empirically in many previous phytosociological tables. The other four options are 50/20, 66/10, 66/20, and 66/33. The most discriminating option is 66/10, which is followed by 50/10, 66/20, 50/20, and 66/33 in that order of discrimination. Thus the first two are the stronger and better criteria for species associations. Application of Rule I in the program involves a comparison of all species occurrences in the program by whatever option is stipulated. Since this is a comparison between rows, Rule I performs an R-type analysis. Associated species cannot be fewer than two species. If a species cannot be grouped with at least a second species according to Rule I, it is rejected as a "single species." In this case it appears in the final table as an ungrouped species together with those initially rejected omnipresent ones.

6.8-2.3 Definition of Relevé or Site Groups. If the sites in which certain associated species occur were known in advance, it would be relatively simple to

search the raw data table for the species that conform to Rule I. This is the technique adopted in a program by Spatz and Siegmund (1973). It would be possible also to develop such a species extraction program in conjunction with the dendrograph technique which allows one to define groups of similar sites. However, using the approach of Ceska and Roemer, relevé groups are defined by the associated species themselves during the operation of the program.

While forming associated species groups in Rule I, the X% part of the option allows species to be absent in some of the sites which are generally common to the group. As the group gains new species, however, it is possible that many of the species could be absent at the same site. To insure that the absences are equitably spread, Ceska and Roemer apply Rule II, which performs a Q-type analysis. This rule stipulates that a site is accepted in the species group if it contains at least X% of the species associated with that group. For reasons of homogeneity, the value of X is the same as in Rule I. If, for example, the 50/10 option is used, a relevé must contain at least half of the species of an associated species group in order to be part of this group of relevés. Rule II therefore imposes a restriction on the method in species-poor areas where sometimes single species are important for community differentiation. However, this restriction is not serious in our analysis as such single species appear in the final table anyway. Such ungrouped species can be used in the species distribution analysis along the transect just as well as the grouped ones. This will be discussed later.

6.8-2.4 Procedure and Sorting Result. The mathematics of the program is quite involved, but the procedure and final outcome can be explained without the mathematical background as follows:

1. The computer selects an initiating species whose relevés form a first tentative relevé group. This initiating species is chosen arbitrarily from the species with high presence throughout the sample set, that is, from those that are present in just under 66% of the relevés.
2. All remaining species are then compared (by R-type analysis) as to their matching occurrences with the first group-initiating species according to one of the options of Rule I. Species that fit the association criterion are temporarily retained; those that do not are temporarily rejected. In this first search process, a number of species may have been found that fit this criterion.
3. The computer then performs a Q-type analysis by scanning the relevés in which

these species occur, and any relevé that contains less than 50% or less than 66% of the species (depending on which Rule I option is applied), is rejected. This is the application of Rule II.

4. The computer then compares the species rows again for their matching occurrences because by rejecting some relevés by Rule II, some species may now fall outside the specific Rule I option. Thus the same option of Rule I is applied in a second computation cycle (i.e. repetition of step 2) and this is followed again in the same cycle by Rule II (i.e. repetition of step 3).
5. Additional computation cycles by an alternation of Rules I and II are performed until all spatially coinciding species are isolated from the set.

It frequently happens that an initiating species is rejected in subsequent computation cycles as single species which then form a one-species group. These single species are listed at the end of the printout table that gives the final results. At the end of this table occur also the originally rejected omnipresent species, and the rare species which are those that occurred only once or twice throughout the entire sample set.

In our example, 169 species were contained in the set of 48 relevés. For this reason, only an extract of the whole table which lists 19 species is here reproduced as Table 6.5. This table extract is sufficient for the purpose of explaining the remainder of our analysis procedure. Table 6.5 shows 4 of the 9 groups that were generated by the 50/10 option of Rule I.

The relevé numbers are listed along the top of the table; the IBP focal site numbers have been added for orientation. The relevés which have been included in the groups are shown in combination with the species which are characteristic of each group. The species are listed (by abbreviated name code) along the left margin of the table. They are separated into the associated species groups. The relevés which make up each group are shown by bracketing the top and bottom of the associated species group with asterisks in the relevé columns. For example, the group at the top of the table consists of relevés 117, 129, 130, 132, 133, 11, 14, 72, 44, 63, 64, 65, 66, 138, 67, 139, and 140 and is characterized by four species (Pellaea ternifolia, Asplenium adiantum-nigrum, Asplenium trichomanes, Agrostis sandwicensis). This has been numbered group 2, based on the order in which it was identified in the computation cycles. The other groups have also been labelled in the output table. The numbers and symbols appearing in each species row are quantitative values (here Braun-Blanquet cover-abundance values) that were recorded for the species at that sample location in the field.

TABLE 6.5. Extract of a final two-way table.

RULES USED:
50 PER CENT INSIDE
10 PER CENT OUTSIDE

IBP FOCAL SITE NO.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
RELEVÉ NO.	004 054 144	049 052 145	018 050 147	019 020 146	021 096 100	092 103 104	083 108 115	024 117 121	081 123 125	077 129 130	075 132 133	011 014 072	044 063 064 065 066 138	067 069 070 139 140 142
SPECIES GROUP														
PELT ER								*		* *	* *	* * *	* * * * *	* * 1
ASPA DI									+	+	+ +	1 1 1	1 + 1 1 1	+ 1
ASPT RI	2						R	+ R		+	+	1 1 1	R R R	+ R
AGRS AN			R					R	+ R	R		1 1 +	+ R	R
								*		* *	* *	* * *	* * * * *	* *
		*	* *							* * *	* * *	* * *		
MACG AH		+	1 1 1							1 1 1	1 1 1	1 + 1		R 1
COPE RN		3	+ + 1						2	1 2 2	1 2 2	2 2 +		
LUZH AW		1	1 2		+				+ 1	1 1 1	+ 1	R +		
RAIC IL	1	R	1							+ + 1	+ 2	1 1 R		
COPM ON				R						1 1 2	1 2 2	2 2 2		
PLET HU			+							+ +	1 + +	1 +		
POLP EL		+ +	1 2							+ +	1 +			
		*	* *							* * *	* * *	* * *		
			* *		* * *	* * *	* * *	* * *	* * *					
HOLL AN		+	+ R	3 2 2	2 1 1	1 2 1	1 1 1	1	1 2 2					
CARW AH		+	R +		2 + 1	1 1	1 2 2	2 1 1	1 1 1		1	+		
ACAK OA	3		2	2 2	5 4 3	3 3 3	4 4 3	5 4 3	3 2					
STYT AM		2	3 3 3		2	1 3	2 2 2	1 2 3	3 2					
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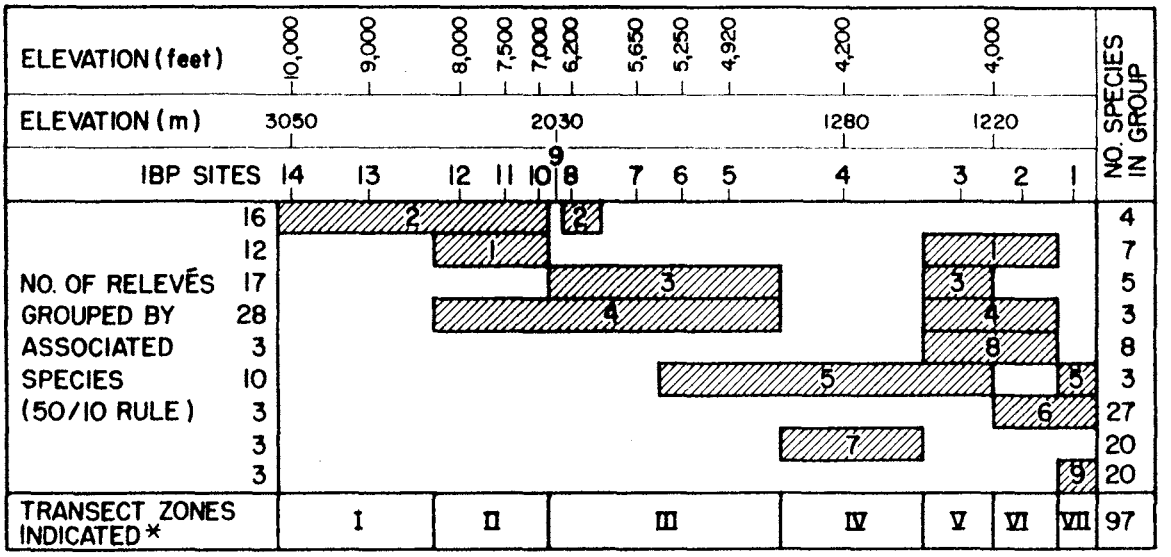
The "dictate" option of the program has been applied in the run which produced Table 6.5. This option allows one to arrange the sequence of samples in any desired order. This is a very desirable feature as it facilitated our data interpretation in relation to the known environmental gradient. As shown at the head of the table the IBP sites are arranged in order from 1 to 14, that is, from the low to the high end of the Mauna Loa Transect. The program may also be used to sort the relevés into a new order forming coherent blocks, a feature useful for other purposes.

6.8-2.5 Extraction of Species Groups into Zonation Diagram. It is now possible to extract the species groups generated by the program into a zonation diagram similar to the way it was done for the clusters of the dendrograph. For this purpose we may ignore the few species occurrences outside the relevé groups. However, they are not ignored in the final analysis as discussed in the next section. Figure 6.11 shows the completed extraction of the 9 groups generated from the 48 relevés. They are here arranged in decreasing altitude from the upper to the lower end of the Mauna Loa Transect. The computer-generated group number is written into each block-graph. The number of relevés that are combined by the group are recorded on the left side. On the right side appear the numbers of species belonging to each group.

We now can apply the same criterion for the definition of transect zones as was applied in the zonation diagram giving the dendrograph results; that is, we can draw a boundary where at least two group (or cluster) limits are indicated by the data. In this case the result is almost identical to that generated by the dendrograph technique, except that the boundary between zones III and IV now coincides with the predetermined boundary. Therefore, it seems valid to accept that boundary in favor of the one generated by the dendrograph analysis.

6.8-2.6 Ordination of Species Distribution along the Mauna Loa Transect. By use of the established transect zones, species groups, and single species it is now a relatively simple matter to diagrammatically demonstrate the important species distribution trends in a form comparable to Whittaker's bell-shaped curves of species distribution along gradients.

This was done by averaging the quantitative value for each species by IBP focal site and by plotting this value over each of these sites along the mountain gradient. Figure 6.12 shows the result for selected native plant species as they



*by at least two group distribution limits

I = Sparse alpine heath scrub

II = Open subalpine Metrosideros scrub-forest

III = Mountain parkland, Acacia koa tree colonies

IV = Sapindus-Acacia koa savanna

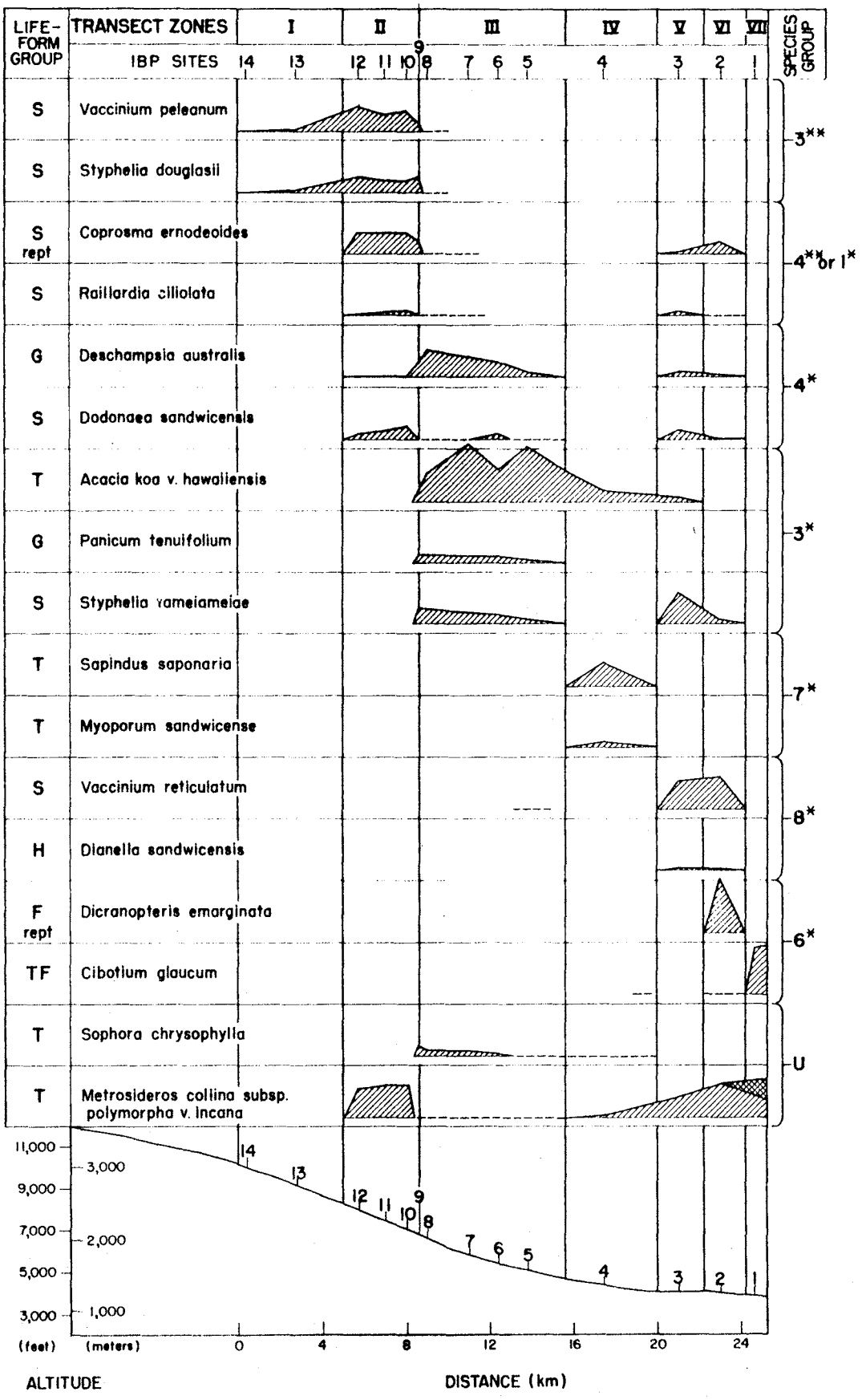
V = Open Metrosideros dry forest

VI = Open Metrosideros rain forest

VII = Closed Metrosideros rain forest

FIG. 6.11. Zonation diagram: altitudinal distribution of associated species groups derived by the two-way table technique.

FIG. 6.12. Distribution diagram of selected native plant species along the Mauna Loa Transect. Transect zones I-VII derived from two-way table analysis. *Members of species groups derived from 50/10 option, **group members derived from 60/10 option, u = ungrouped species. Dashed lines mean "present," but not recorded in relevés or rare in relevés.  Metrosideros collina subsp. polymorpha var. macrocarpa. Life-form symbols: S = shrub, rept = reptant or creeping, G = grass, T = tree, H = herbaceous plant other than grass, F = fern, TF = tree fern.



Vertical scale for each species I } 50% average shoot or crown cover

occur along the Mauna Loa Transect.

In contrast to Whittaker's form of presentation, species population curves were not smoothed into bell-shaped curves. Instead, population quantities within species were connected by straight lines--a minor difference. However, our diagram incorporates three major departures from Whittaker's diagrams:

(1) Individual species population curves are shown separately. This provides for a clearer overview than a plot of several species on the same base line and y-axis segment.

(2) Species population curves are ordinated by amplitude restrictions from the left side of the graph (high altitude species, group 3) to the right side of the graph (rain forest species, group 6).

(3) All quantitatively important plant life-forms are admitted to the test; the test is thus not restricted to woody plants as in Whittaker's diagrams.

The group numbers on the right side of the diagram (Fig. 6.12) are the computer-derived numbers from the two-way tables. Here groups were utilized from two Rule I options, namely from the 66/10 and 50/10 options. In addition, two ungrouped or single species are shown at the bottom of the diagram. In contrast to the zonation diagram (Fig. 6.11), species ranges extending beyond the group limit are shown in the distribution diagram (Fig. 6.12) exactly as they were recorded in the field. Dashed lines indicate rare occurrences either in the relevés or as observed outside. It is of interest to note here that the greater population quantities of most species occur inside the group limits. This is of interest insofar as the two-way table analysis generates a quantitative sorting in spite of being operated by only presence and absence criteria in this program.

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